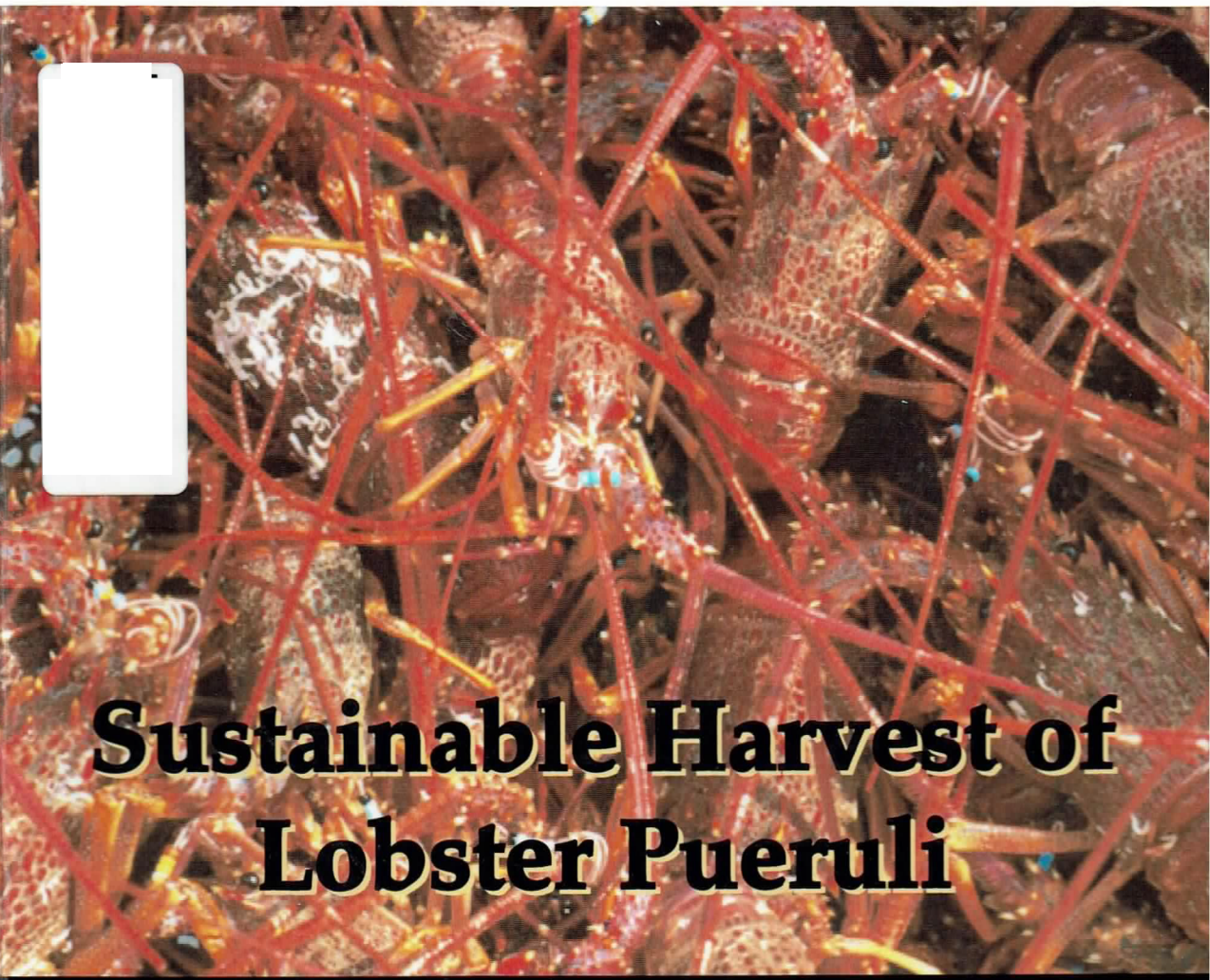

Sustainable Harvest of Lobster Pueruli

A Way Forward for Rock Lobster Aquaculture

David J Mills BSc (Hons)

In fulfilment of the requirements of the Degree of Doctor of Philosophy
University of Tasmania (May 2005)

Declarations

Statement of originality

This thesis contains no material that has been accepted for a degree or diploma by the University or any other institution. To the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text.

11/11/05

David Jonathan Mills

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Abstract

A major impediment to the development of spiny lobster aquaculture has been the inability to rear lobsters from eggs, through the delicate larval stages, to the settling puerulus stage. An alternative is to harvest pueruli from the wild for commercial on-growing. However, wild harvest of pueruli can potentially have a deleterious effect on the adult lobster fishery. Research presented here investigates both the feasibility and sustainability of an industry based on the harvest of southern rock lobster (*Jasus edwardsii*) pueruli.

Pueruli were found to settle on a diverse range of substrata. Cheap, lightweight puerulus collectors constructed from readily available materials, such as trawl netting and shade cloth, proved to be significantly more cost-effective for large-scale harvest than collectors currently in use for scientific monitoring of puerulus settlement.

A system of 'reseeding' wild habitat with hatchery-reared juveniles was evaluated as a method of ensuring sustainability of wild populations. Reseeding involves the release of a portion of on-grown (naïve) juveniles after one year to compensate for those that would have survived in the wild, and its success is predicated on high survival among released juveniles.

Naïve juvenile lobsters tracked acoustically behaved in a similar manner to wild animals, sheltering in appropriate hides during the day, often co-habiting with wild conspecifics, and then moving at night. The highest levels of activity occurred in the 12 h following release, while the distances moved by individual lobsters declined rapidly after this initial period. Stomach contents of tracked lobsters recaptured after 11 days revealed that naïve lobsters adapted well to wild food sources, although their diet differed from that of wild lobsters.

Mortality rates of tethered juvenile lobsters varied substantially between sites in southeastern Tasmania. However, these differences

were not significant once results were corrected for experimental artefacts associated with differences in the predator assemblages among sites. Video footage of tethering trials showed that large wrasse and small octopus were the major predators of juvenile lobsters. Crabs and large lobsters also captured tethered juveniles, however experiments in a mesocosm showed that these captures were artefacts of tethering.

Survival of naïve lobsters estimated from mark-recapture trials was generally equivalent to that of tagged wild lobsters. An exception was where lobsters were released onto a small area of isolated patch-reef. Here, naïve lobsters tended to ignore reef boundaries, moving away from shelter and onto sand. These results suggest that by following simple criteria in the selection of release sites, mortality among released naïve lobsters is minimal, and equivalent to that of wild juveniles at the same stage. The overall conclusion is that reseeding is an effective method of compensating for puerulus harvest.

Statement of co-authorship

Chapters 2-7 of this thesis have been prepared as scientific manuscripts as identified on the title page for each chapter. In all cases experimental design and implementation of the research program, data analysis, interpretation of results and manuscript preparation were the primary responsibility of the candidate, but were carried out in consultation with supervisors, and with the assistance of co-workers. Contributions of co-authors are outlined below:

Chapter 2:

Dr Bradley Crear (Tasmanian Aquaculture and Fisheries Institute (TAFI)) led the lobster aquaculture research team at TAFI when this research was conducted. Dr Crear and his research group provided financial assistance as well as technical support for the conduct of field-based puerulus collector trials.

Chapter 3:

Dr Caleb Gardner (TAFI) is a supervisor for this Ph.D. program. He provided advice in the areas of experimental design, and lobster biology and ecology, as well as assisting with the field program.

Samuel Ibbott (TAFI) has extensive experience diving around the coast of Tasmania and provided invaluable advice on site selection, as well as assisting in the field program.

Chapter 4:

Gerald Verdouw (SciElex Pty Ltd) manufactured electronic components and provided engineering expertise in the configuration and construction of the camera system.

Dr Stewart Frusher (TAFI) received a grant from the Ian Potter Foundation to finance the construction of the camera system, and provided advice on system requirements.

Chapter 5:

Dr Craig Johnson (School of Zoology – University of Tasmania (UTAS)) is a supervisor for this PhD program, and

provided advice on experimental design and statistical analysis of results.

Dr Caleb Gardner (TAFI) provided advice in the areas of experimental design and lobster biology.

Chapter 6:

Dr Caleb Gardner (TAFI) provided guidance on mark-recapture techniques and analysis, and assisted in the field program.

Megan Oliver (National Institute of Water and Atmospheric Research – New Zealand) is a collaborator specialising in lobster behaviour research, and provided critical advice in this area.

Chapter 7:

Dr Caleb Gardner (TAFI) provided guidance on mark-recapture techniques, analysis and lobster ecology, and assisted with the field program.

Dr Craig Johnson (School of Zoology – UTAS) provided advice on experimental design and statistical analysis of results.

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My supervisors, Caleb Gardner and Craig Johnson have been fantastic mentors throughout this project, and their advice has added greatly to its outcomes. I thank Caleb particularly for attracting funding necessary for much of this research, providing encouragement and support throughout the process. I thank Craig for being an excellent mentor in quantitative ecology, and for his scientific editing and proofing abilities that are second to none. I thank Caleb and all members of the Crustacean Research team at TAFI for providing an excellent working environment in which to complete this research.

The acoustic tracking, tethering and mark-recapture studies were at times extremely labour intensive, and would not have been possible without field teams that were prepared to 'go the extra mile' often diving for long hours day or night when the water (down to 8°C) was warmer than the air. Particular thanks go to Sam Ibbott, Shane Fava, Pip Cohen, Robbie Kilpatrick, Carl Waterworth, Bradley Crear, Craig MacKinnon and Simon Wilcox.

Most importantly I thank my family, Kate, Emily and Jacob, for their unending support, love, encouragement and patience throughout this process. To Kate, I would not have got to this point without your help, both in doing more than your share of parenting, as well as putting in the late nights of proof-reading. I guess I'm cooking dinner for the next year?

Contents

Chapter 1

General introduction

1.1 Background

Despite increased fishing pressure and improvements in harvest efficiency, global production of spiny lobsters has plateaued (FAO 2004), with most fisheries fully or over exploited. Among possible methods for increasing production or alleviating pressure on fisheries are fishery enhancement and aquaculture (Herrnkind et al. 1997, Phillips & Evans 1997, Booth & Cox 2003). Spiny lobsters are an attractive prospect for aquaculture due to their high market value. In addition, recruitment limitation, which is a critical pre-condition for successful stock enhancement programs (Doherty 1999), has been demonstrated for several species (Caputi et al. 1995, Butler & Herrnkind 1997). However, progress in the areas of stock enhancement and aquaculture has been hampered by the difficulties associated with larval rearing.

Early successes in the culture of spiny lobsters through to settling pueruli (Kitaka 1988) have not been widely replicated. While several species, including *Jasus edwardsii* (Illingworth et al. 1997, Ritar & Smith 2005), have now been cultured from eggs through to pueruli in research facilities (Kittaka 1988, Kittaka et al. 1988, Kittaka & Kimura 1989), commercial-scale production has proven elusive due to the extreme fragility of the spider-like phyllosoma larvae and protracted nature of their larval duration. Under laboratory conditions larval development for most species takes in excess of 300 days (e.g. Kittaka et al. 1988, Illingworth et al. 1997) and survival of any larvae through to metamorphosis is rare.

In contrast to the difficulties associated with larval rearing, lobster post-larvae are robust and adapt well to intensive culture conditions. Survival rates of 90-95% per annum and growth to a marketable product in 2-3 years can be expected (Phillips et al. 1983, Crear et al. 1998, Geddes et al. 2001). Clearly, if difficulties associated with larval supply can be circumvented, there is considerable potential for industry expansion. For this reason the idea of harvesting pueruli from the wild for on-growing to a marketable product has gained momentum (Booth & Kittaka 1994, Jeffs & James 2001).

Historically, collection of wild seed has provided the basis for profitable aquaculture operations, and in some instances generated income to finance the development of hatchery-based rearing techniques. The most prominent examples are in shellfish culture and include mussel, oyster and scallop operations. However, throughout Asia and South America the culture of shrimp (Larsson et al. 1994, Primavera 1998) and many finfish species (Hair et al. 2002, Durville et al. 2003) also rely on wild collection of larvae or juveniles. The efficacy of on-growing wild-caught seed as a method for increasing production arises from the disparity between high mortality of post-larval and juvenile stages in the wild (Phillips et al. 2003, Doherty et al. 2004) and high survival among the same stages in hatchery conditions. If seed can be collected from the wild prior to survival 'bottlenecks', and maintained in culture with high survival rates, production can be increased.

1.1.1 Collection of lobster pueruli

For more than 30 years scientists have deployed puerulus collectors in coastal areas for the purposes of monitoring settlement patterns and studying the early life history of lobsters (e.g. Witham et al. 1968, Phillips 1972, Booth & Tarring 1986). Similar research on a variety of species has lead to a diverse range of collector designs, each optimised for catching a particular target species (see review by Phillips & Booth 1994).

The earliest reports of commercial harvest of pueruli for on-growing purposes come from Vietnam in 1992 (Tuan & Mao 2004). This industry has developed rapidly since 1996, and output was recently estimated at 2000 tonnes yr^{-1} (Thuy & Ngoc 2004) from 4000 producers holding ca. 35 000 on-growing cages (Tuan & Mao 2004). This compares with wild-fishery production from Vietnam that peaked at 500-700 tonnes in the 1980s (Tuan & Mao 2004). Puerulus and post-puerulus lobsters are collected by night time use of purse seine nets with an electric light attractant, by diving, and by a range of passive collectors built from dead coral or bunched-up fishing nets. This industry has created employment and improved socio-economic conditions in coastal communities (Thuy & Ngoc 2004). A particular advantage of puerulus collection over hatchery-based larval rearing is that it does not require large

capital outlay, and can use low-technology methods that are suitable for use in poorer and developing countries.

Commercial harvest of pueruli was first permitted in New Zealand in 1996 (Jeffs & Hooker 2000). Permit conditions allow for a maximum of 400 000 pueruli to be collected in any year, and a maximum of 80 000 by any individual licence holder. Permit holders have been restricted to using 'crevice' type collectors (Booth & Tarring 1986), limiting the potential for the development of more cost-effective techniques. Early attempts at establishing land-based grow-out facilities proved unprofitable (Jeffs 2003), however, more recently experimental-scale trials of sea-cage based culture systems have shown considerable promise (Jeffs & James 2001).

Following protracted negotiations between fishery managers and the aquaculture and fishing industries, permits for puerulus collection were issued in Tasmania in 2001. Initially seven permits were issued, each allowing the collection of 50 000 pueruli yr^{-1}. Collector designs were not specified under permit conditions. It is now apparent that most of the permit holders were 'speculating' that the industry may develop, but were unprepared to inject any capital into development. Consequently, after 2-3 years of little progress, five permits were not renewed. The remaining two permit holders continue to experiment on a small scale with methods of puerulus collection. Permit holders cited restrictive permit conditions and the (overly optimistic) expectation that the development of hatchery-based culture was imminent, as the main reason for not persevering with collection trials.

Commercial on-growing of pueruli or juvenile lobsters has also been reported from the Philippines (Arcenal 2004), the Solomon Islands (Hair et al. 2004), and Taiwan (Juinio-Menez & Gotanco 2004), while research and experimental-scale trials are being conducted in South Africa (Bailey & Fielding 2002, McVeigh 2002, Dubber et al. 2004), India (NIOT 2004), the United States of America and the Caribbean (Harris 2005, J Mattias, Posseidon Science Group, New York. pers comm).

1.1.2 Ensuring sustainability

Where populations are structured predominantly by recruitment levels rather than density-dependent factors, the removal of pueruli has the potential to reduce adult stocks. Varying degrees of recruitment limitation in spiny lobsters have been either demonstrated by direct habitat manipulation (Butler & Herrnkind 1997) or implied from the relationship between puerulus settlement and numbers of lobsters recruiting to the fishery in subsequent years (Caputi et al. 1995, Gardner et al. 2001). Where active fisheries for adult lobsters exist, it is clear that capture of pueruli for aquaculture in the face of evidence of recruitment limitation in the fishery, poses a significant hurdle that must be overcome for both political reasons and a biological imperative to protect stocks. Opposition from high-value fishing sectors has the potential to derail any attempts to establish an industry based on puerulus harvest, and this will only be overcome by demonstrating that pueruli can be harvested in a way that does not place further pressure on stocks.

As most established fish and crustacean aquaculture operations relying on wild seed harvest are based in developing countries with rudimentary fisheries management systems, little attention has been paid to the management of collection practices. The consequences of this have, at times, been severe. The harvest of shrimp seed in Ecuador, the Philippines and Thailand has significantly reduced penaeid stocks and affected wild fisheries (Cobo 1988, Dierberg & Kiattisimkul 1996, Primavera 1997). Indiscriminate harvest of all sizes of lobsters for fattening in cages has lead to a collapse of this industry as well as the wild lobster fishery in many areas of the Philippines (Arcenal 2004, Juinio-Menez & Gotanco 2004). Similarly, declines in catches of adult rock lobsters in Vietnam have coincided with an increase in puerulus harvest (Thuy & Ngoc 2004), although no causal link has been demonstrated in this case.

Managers of lobster fisheries in Australia and New Zealand have committed to addressing these potential problems through a process termed 'biological neutrality', which requires some form of compensatory process to counteract the increased fishing mortality

caused by puerulus harvest. The most appropriate compensatory mechanism for a given fishery will depend on both the biology of the species concerned, and the fishery management system in place. Estimates of survival of juvenile *Panulirus cygnus* in Western Australia indicated that there was a high density-dependent component to natural mortality in the first year post-settlement and consequently even large harvests of puerulus would be expected to have negligible impact on wild fisheries (Phillips et al. 2003). In New Zealand, estimates of natural survival of *Jasus edwardsii* from puerulus through to fishery recruits were used to develop a quota buy-back system whereby the retirement of one tonne of commercial quota from the fishery enabled the capture of 40,000 puerulus (Jeffs 2003). Approaches relying on effort reduction will only be effective in fisheries where management practices allow effort to be regulated effectively, which excludes many developing countries. The development of a system for managing puerulus harvest, which is effective independently of methods used to regulate the adult fishery, stands to benefit both the wild fishery and culture industries in developing countries.

A system of 'reseeding' was adopted as part of licence conditions to achieve biological neutrality in Tasmania. This involves on-growing harvested pueruli for one year, then releasing back to the area of capture a proportion of juveniles estimated to be equivalent to the number that would have survived naturally. This system of management is underpinned by a large discrepancy in natural mortality (95-97%; Herrnkind & Butler 1994, Edmunds 1995) and captive mortality (5-15%; Phillips et al. 1983, Kington 1999, Crear et al. 2003) during this period so that, following reseeding, a large proportion of juveniles are still available for on-growing in captivity to a marketable product. While the Tasmanian fishery is regulated by an individually transferable quota system, there are several reasons to favour reseeding over quota buy-back:

1) In some areas of Tasmania sub-legal female lobsters contribute significantly to egg production. Under a quota buy-back scheme this egg production would be lost for lobsters that would have survived through to recruitment, but are instead held in culture facilities;

2) Reseeding provides the ability to spatially manage the effects of puerulus harvest (release locations can be specified) in a fishery with no spatial regulation;

3) Calculation of the number of lobsters to be released is based on estimates of survival for the first post-settlement year only, rather than from settlement to recruitment to the fishery, thus reducing uncertainty in the estimate of compensation;

4) Reducing the total fishery quota is likely to result in a reduction of effort in areas that are exposed and difficult to access, whereas puerulus collection by its nature must occur in sheltered and accessible inshore waters. This would place additional pressure on the most heavily exploited component of the Tasmanian resource; and

5) There is no negative socio-economic impact on fishing communities as the aquaculture industry is created without reducing the size of the fishery.

The success of reseeding as a compensatory mechanism is predicated on high survival of lobsters released back to the wild. A similar system termed 'nature tithing' was trialled in the Philippines, under which 10% of adult lobsters from farms were released into designated sanctuary areas to compensate for juvenile harvest and increase spawning biomass. However, they found that released lobsters were susceptible to predation as they *"....forgot for some days that they were supposed to be a nocturnal species"* (Arcenal 2004). This experience highlights the greatest potential impediment to the effectiveness of reseeding, namely that hatchery-reared individuals frequently display behavioural or morphological traits that make them less suited to survival in the wild than their wild counterparts (Olla et al. 1994, 1998, Berejikian 1995, Svåsand et al. 1998, Kellison et al. 2000, Brown & Day 2002, Hossain et al. 2002, Davis et al. 2004). Research methods that can provide a clear indication of survival of released animals in the wild will provide a good measure of the likely success of this management system.

1.2 Study objectives

A major limitation to developing lobster aquaculture industries in many countries, including Australia, is the inability to efficiently collect sufficient numbers of pueruli in a sustainable manner. This study aims to address these issues by:

1) Designing a cost-effective collector for the commercial harvest of *Jasus edwardsii* pueruli; and

2) Assessing the suitability of reseeding as a mechanism to compensate for the commercial harvest of pueruli by:
    i) Comparing habitat use, movement, feeding and survival of reseeded, on-grown lobsters with that of wild conspecifics; and
    ii) Identifying predators of juvenile lobsters, and assessing spatial variability in predation and survival rates at sites in SE Tasmania.

1.3 Approach and thesis structure

The success of the lobster culture industry in Vietnam is to a large degree due to the implementation of low-technology, and therefore inexpensive, techniques for both collection and on-growing. Most collectors currently in use for collecting *Jasus edwardsii* pueruli were designed for scientific research rather than as commercial devices, and are not an economically efficient means of collecting pueruli (Jeffs 2003). In Chapter 2, I investigate the cost-effectiveness of simple, lightweight collectors constructed from readily available materials, which can be deployed on long-lines for efficient servicing.

Reseeding has been identified as the most suitable method for managing the sustainable harvest of pueruli in Tasmania, and is likely to be the only workable method in developing countries where fisheries are rarely managed with effective effort controls.

Critical to the success of this method is an understanding of the fate of reseeded lobsters. To obtain this information in the field under natural conditions there is no alternative but to follow individually marked animals through time (Lebreton et al. 1992). I employed two different but complementary approaches to achieving this; observing the behaviour and ecosystem interactions of a small number of individuals in detail (Chapters 3, 4 and 5), and estimating survival parameters for a larger number of lobsters followed at a lower temporal resolution (Chapters 6 and 7).

Chapter 3 provides the first indications of the likely response of wild and naïve juvenile lobsters to capture, tagging and release. Juvenile lobsters were tracked using acoustic tags to provide information on movement, habitat use and feeding patterns. Information gained in this experiment was critical to the design and implementation of pilot-scale release trials reported in Chapters 6 and 7.

Details of the design and construction of an infrared capable multi-camera system are provided in Chapter 4. This system was employed in Chapters 5 and 7 to monitor the behaviour and predator interactions of tethered or released juvenile lobsters.

Choice of appropriate release sites is critical to the effectiveness of reseeding programs. In Chapter 5, I report the results of video-monitored tethering experiments used in combination with mesocosm trials to assess differences in predation pressure at multiple sites, and identify likely predators of juvenile lobsters. This chapter presents a comprehensive analysis of the artefacts associated with tethering experiments.

Chapter 6 incorporates information on lobster movement and behaviour obtained in previous experiments into the design of a mark/recapture trial aimed at assessing the relative survival of tagged wild and naïve juvenile lobsters. Chapter 7 reports on the extension of this work to multiple sites, and further uses acoustic tracking and caging trials to investigate movement and mortality immediately following release.

The reader should note that Chapters 2-7 were prepared as scientific manuscripts, and accordingly some repetition, particularly in chapter introductions, was unavoidable.

A CD containing video footage from the study has been included inside the back cover of this thesis. Videos included show some of the methodology employed, as well as providing the reader with a first-hand look at the behaviour of lobsters (tethered and released) and their predators (all videos © TAFI, 2005).

Chapter 2

Developing a cost-effective collector for commercial harvest of lobster pueruli

This Chapter previously published as:

Mills DJ, Crear BJ (2004) Developing a cost-effective puerulus collector for the southern rock lobster (*Jasus edwardsii*) aquaculture industry. Aquac Eng 31:1-15

Abstract

Due to the extended duration of larval development, commercial rock lobster aquaculture is proceeding through the harvest of wild pueruli. Puerulus collectors appropriate for commercial use were developed by: *(i)* obtaining information on appropriate collection materials from industry and past research; *(ii)* directly comparing catch rates from these materials; and *(iii)* designing and comparing collectors appropriate for large-scale commercial deployment built with selected materials. *Jasus edwardsii* pueruli settled on a variety of materials often bearing little resemblance to their natural habitat. 'Bottlebrush' collectors constructed from shade cloth and PVC conduit proved robust, easy to service and were relatively cost effective. 'Sandwich' collectors with filamentous material caught most pueruli, and required a shorter conditioning time than other collectors, but were heavy and relatively expensive to build. Loss of pueruli from collectors being hauled to the sea surface was minimal. Whilst providing details for the construction of cost-effective collectors, we also advocate a 'hands on' approach to designing collectors based on materials readily available to prospective farmers.

Keywords: Spiny lobster culture, *Jasus edwardsii*, puerulus collectors

2.1 Introduction

As ongoing and intensive efforts to culture spiny lobster pueruli in commercial quantities have resulted in the production of only a handful of individuals (see Kittaka 1994), the idea of harvesting pueruli from the wild for on-growing to a marketable product has gained momentum (Phillips & Evans 1997, McVeigh 2002). Collectors designed to capture the puerulus stage of spiny lobsters (Palanuridae) have been used successfully by scientists to study recruitment processes (Jernakoff 1990, Phillips et al. 1991, Booth et al. 2001) and have shown promise as a predictive tool in fisheries management (Phillips 1986, Breen & Booth 1989, Gardner et al. 2001). While the body of literature on scientific puerulus collectors (see review by Phillips & Booth 1994) provides a useful starting point for the development of commercial collectors, desirable properties of commercial and scientific collectors differ. Specifically, maximising precision is vital for scientific collectors, but is of little importance for commercial collection. Instead, the highest priorities for commercial collection are cost effectiveness of collector construction, deployment and servicing.

An example of these conflicting priorities is evident in the methods commonly used for deploying and servicing research collectors in New Zealand and Australia (Booth & Tarring 1986, Gardner et al. 2001). Crevice collectors are attached individually to heavy mooring blocks. During servicing, divers cover each collector with a fine mesh bag, eliminating escapement, and maximising precision. Neither the expense of individual mooring blocks, nor the time taken for divers to bag and service collectors is conducive to cost efficient commercial operations to obtain wild pueruli, especially given that the catch per collector is normally quite low.

This study was initiated in response to requests from prospective puerulus harvesters for the development of collectors that could be deployed on longlines and serviced safely from small (6-8 m) workboats. Puerulus settlement is distinctly seasonal and interannual variability can be extreme (Booth et al. 1991, Gardner et al. 2001). Accordingly, the commercial viability of collection

operations may hinge on using vessels and equipment already in service on marine farms that can be used for other tasks when settlement is low.

Here we report on a 3-stage approach taken to the development of commercial puerulus collectors. First, information was sought on cheap and readily available materials that were likely to provide a suitable settlement substratum for pueruli. Second, catch rates of candidate materials were directly compared in a field trial using identical deployment methods, and third, collectors appropriate for commercial use were designed using the best performing materials, and compared in field trials. Further, we addressed a major issue of cost efficiency in servicing by examining the rate of loss of pueruli from collectors as they are hauled from the seabed to the surface.

2.2 Materials and methods

2.2.1 Stage 1: Material selection

Operators from coastal marine industries have reported that pueruli settle readily on a diverse range of submerged structures. A survey was sent to marine farmers asking them to indicate structures on which puerulus settlement had been observed, the location and depth of settlement, and on the numbers of pueruli seen. An identification sheet was provided which included drawings of a *J. edwardsii* puerulus and a squat lobster (family Galatheidae), to avoid misidentification (see Mills & Crear 2001).

2.2.2 Stage 2: Comparison of materials

For robust comparisons, we required a uniform test structure capable of containing any of the chosen materials. As survey returns indicated that pueruli frequently settled in sub-tidal oyster cages, the basket system used for oyster grow-out in Tasmania was adopted. This consists of plastic mesh baskets hung vertically on a ladder made from rope and timber (Fig. 2.1). This system provides a large settlement area to increase catch rates while still maintaining small sub-units that are easy to handle. Each ladder contained a single trial substratum type to avoid possible

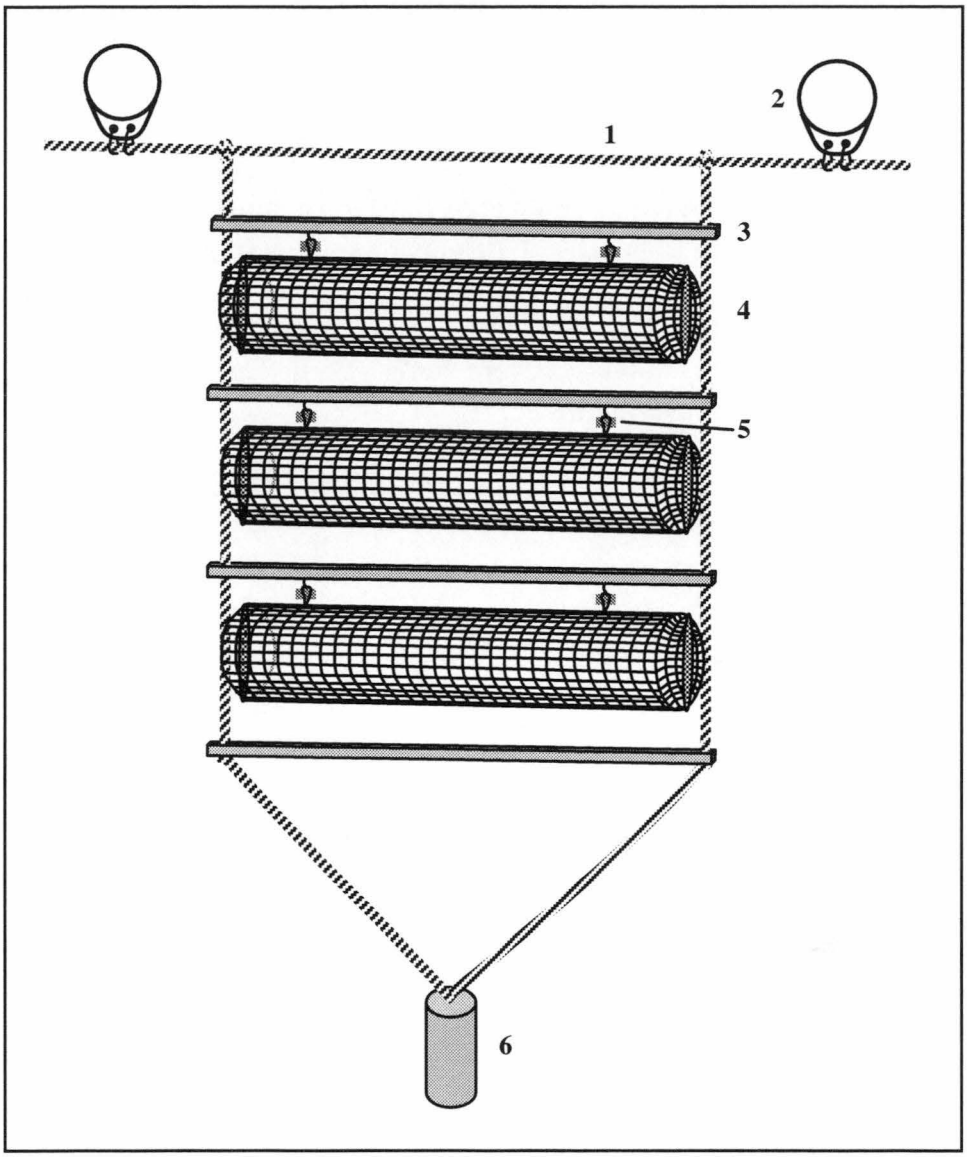

Fig. 2.1 Material trial collector design after oyster grow-out baskets used in Tasmania. 1) Surface backbone rope 2) Surface buoys 3) Timber ladder rungs 4) Mesh baskets containing experimental materials 5) Toggle system for attaching baskets to ladders 6) 2-4 kg weight.

confounding effects of position on the ladder, and each entire ladder was treated as a single sampling unit.

Baskets were constructed from a 1.0 x 0.8 m section of 12 mm (mesh size) plastic oyster mesh. The mesh was rolled along its long

axis with overlapping edges secured by cable ties to produce a cylinder of approximately 0.25 m diameter. One end of the cylinder was closed off with cable ties, and the other by a plastic clip to allow removal and clearing of the trial materials.

Each ladder included 4 timber rungs 1.2 m long, hung at 0.5 m intervals between 2 lengths of 10 mm rope. A system of toggles and loops allowed baskets to be easily removed from rungs for servicing. A 2-4 kg weight was suspended from the bottom of each ladder to stabilise collectors. Ladders were hung every 2 m along a 30 mm rope buoyed at the sea surface.

Four trial materials were selected based on feedback from the industry survey:

1) Empty oyster shells were obtained from local oyster processors and placed in baskets in similar numbers to that seen commonly on oyster farms (filling approximately 1/3 of the basket);

2) Discarded heavy deep-sea trawl mesh (8mm braided polyethylene, 120 mm mesh size) was obtained from fishing companies. A 1 m^2 section was placed in each basket;

3) Discarded light gauge 'market trawl' mesh (64 ply (approx. 1.5 mm) polypropylene, mesh size 60 mm) was obtained from fishing companies. A 1 x 2 m section was placed in each basket;

4) Black wind-break mesh (Sarlon Industries Pty. Ltd. Australia, product no. 648030, similar to mesh used in onion bags), was bunched up to provide darkened spaces of similar size to those found in droplines of mature cultured mussels. Four sections of 1.8 m x 0.4 m mesh were placed in each basket.

Four ladders of each material type were deployed at 3 sites on the east and south east coasts of Tasmania highlighted in the industry survey as areas with comparatively high settlement: Garden Island

(147° 51.935'S, 43° 7.938'E), Port Arthur (147° 7.958'S, 43° 15.43'E) and Great Oyster Bay (148° 12.553', 42° 6.725'E).

Collectors were serviced monthly using a 7 m aluminium boat. The rope backbone was lifted to the gunwale and ladders brought onboard in turn. Contents of the mesh and shade cloth cages were removed and shaken over a large tub, the contents of the tub poured through a sieve and the pueruli removed. Oyster shells were emptied onto a sorting tray for inspection.

2.2.3 Stage 3: Collector trials

Five collector designs were compared in 2 trials conducted during peak settlement periods of 2 consecutive years. Trials were conducted in Waubs Bay, Bicheno (41° 52.343'S, 148° 17.918'E) on Tasmania's east coast, an area of consistently high puerulus catches (Kennedy et al. 1994). The site was on unstructured sand at a depth of 10 m. Collectors were attached at spacings of 3-4 m to a ground-chain linking moorings in place from a previous experiment. Collector positions on the site were randomised for each monthly sample to avoid confounding due to collector interactions (see Phillips et al. 2001). All collectors were deployed 3 months prior to commencing monthly sampling to allow for a build-up of biofouling 'conditioning', which is important for collector performance (Phillips & Booth 1994). Monthly sampling involved divers retrieving collectors, and attaching them to a line to be hauled to a servicing vessel. On the vessel, pueruli were removed from collectors and staged using the 4-stage system after Booth (1979).

Collectors were tested in 2 trials over peak settlement periods in consecutive years. The size of collectors for Trial 1 was standardised to 0.4 m^3. Designs were:

1) Floating crevice collectors (Fig 2.2A): Crevice collectors (Booth & Tarring 1986) have proven successful for scientific monitoring of *J. edwardsii* puerulus settlement in southern Australia (Kennedy et al. 1991) and New Zealand (Booth et al. 1991). A free-floating variant of this collector described by Booth et al. (1991) may be practical for commercial

harvesting, as they can be deployed on long lines. Floating crevice collectors were constructed with 16 squares of CCA-treated (chromated copper arsenate) marine plywood, each 400 x 400 x 9 mm, held in a galvanised steel frame with a steel bolt passing though the 4 corners of each sheet. PVC conduit spacers (25 mm) placed over the bolts at alternate ends of each sheet produced 15 wedge-shaped crevices suitable for pueruli settlement. Four 200 mm diameter trawl net pressure floats were tied to the top of each collector, and a mooring rope with swivel to the bottom.

2) Floating crevice collectors with carpet surfaces: Once deployed, crevice collectors can take many months to condition and catch maximum numbers of pueruli (Booth 1979, Kennedy et al. 1994). Gluing carpet tiles to the settlement surfaces of crevice collectors was seen as a way of providing 'artificial conditioning'. These collectors were constructed and deployed as above, but with a 0.4 m^2 carpet tile glued to each settlement surface.

3) Mesh collectors (Fig. 2.2B): Substratum trials showed that light-gauge trawl mesh was effective at catching pueruli. A 0.4 m cube of stiff plastic 'garden trellis' mesh (mesh size approximately 40 mm) was constructed by joining the edges with cable ties. One side of the cube was secured with removable plastic clips to allow internal mesh to be removed and serviced. Each cage was filled with a 2 m^2 piece of light trawl mesh and a 200 mm diameter foam float. A mooring rope with swivel passed diagonally through each cube and was attached at top and bottom corners.

Eight of each of the test collectors were deployed along with 3 standard crevice collectors, which were included to provide an indication of puerulus abundance during the trials. Standard crevice collectors were not included as a full treatment in the experiment as they cannot be deployed on longlines, and hence do not meet the criteria suggested for commercial collectors by prospective industry participants. Standard crevice collectors were

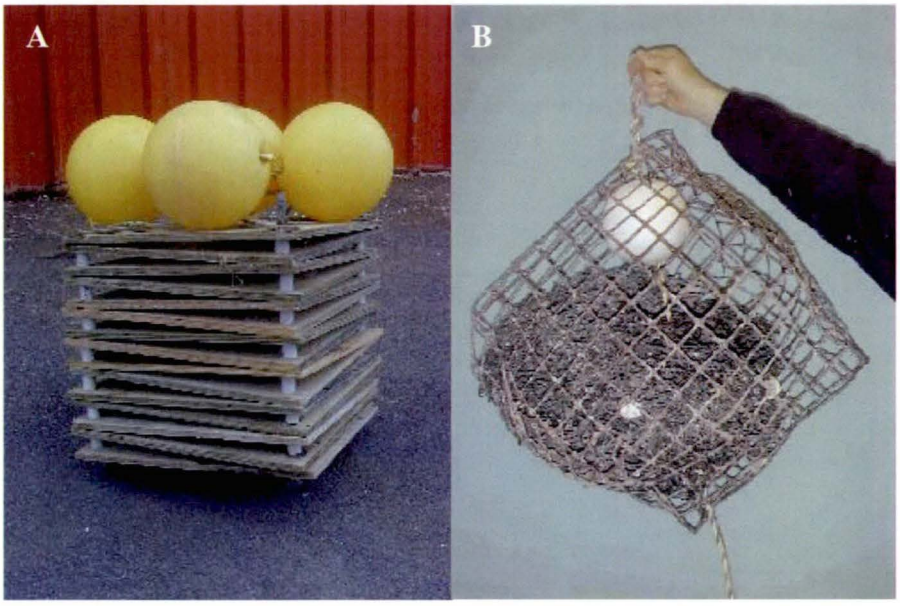

Fig. 2.2 A) Floating crevice collector B) Mesh collector with internal float.

moved from a site within 500 m and had been deployed and conditioning for 2 years previously.

The most successful collector from Trial 1 was compared with 2 further designs in a second trial:

1) Bottle-brush collectors (Fig. 2.3a): Each collector comprised 10 rosettes made from a 1.8 x 0.4 m strip of black windbreak mesh (Sarlon Industries Pty Ltd Australia, product no. 648030). Each strip of mesh was folded concertina-style and pinched at its centre to form a 'rosette' approximately 0.4 m diameter. Rosettes were cable-tied at 50 mm spacings along a 0.5 m length of 15 mm diameter PVC conduit. Spaces within rosettes and between adjacent rosettes formed appropriate sized hides for pueruli. A 200 mm diameter styrofoam float was tied to the top of the conduit, and a mooring rope with swivel to the bottom. Bottlebrush collectors were serviced by shaking vigorously over a 250 L plastic bin.

2) Sandwich collectors (Fig 2.3b): These were modified versions of the 'sea-weed' collector designed for catching *Sagmariasus verreauxi* (Syn. *Jasus verreauxi*) pueruli in New South Wales (Montgomery & Craig 1994). They use the same collection materials as Phillips collectors (Phillips 1972) which are used successfully for *P. cygnus* pueruli in Western Australia. Collectors in this trial were identical to those used by Phillips et al. (2001) for commercial harvesting trials with *P. cygnus*.

Collectors were built from two sheets of grey industrial P.V.C. (615 x 350 x 4.5 mm) held apart at their ends by 2 timber braces (47 x 45 x 38 mm). Twenty five tassels of polyethylene split fibre 125 tex (Kinnears Pty Ltd, Victoria, Australia) were attached to the outer surface of each sheet. These fibres are used for making 'silver' rope, and a tassel looks like several unravelled lengths of rope bundled together. Two 250 mm diameter floats were attached to 1 timber brace, and a bridle to a mooring line with swivel on the other. Sandwich collectors were serviced by spinning rapidly on a purpose-built jig.

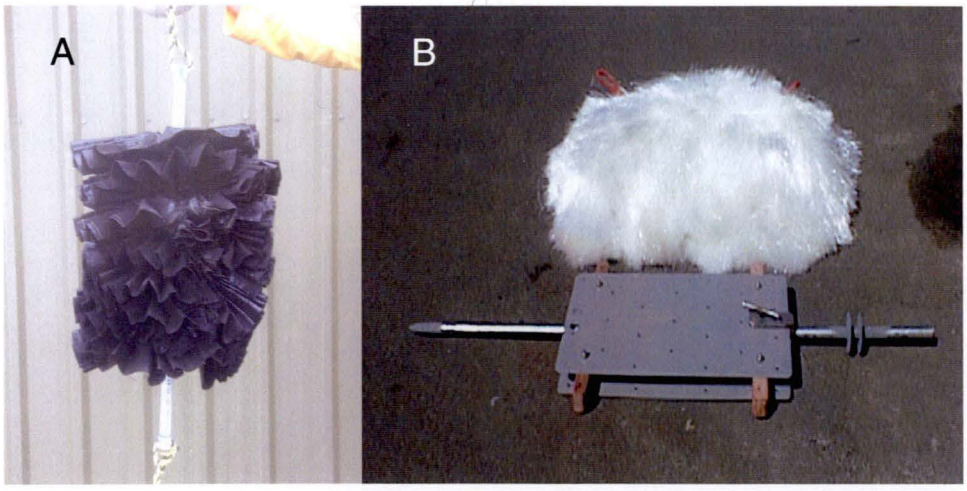

Fig. 2.3 A) Bottlebrush collector B) Sandwich collector with (above) and without (below) fibre tassels attached. The shaft used with the spinning jig is shown with the lower collector (photo M Rossbach).

2.2.4 Collector cost efficiency

Cost efficiency of puerulus collection will be influenced by the cost of constructing, servicing and maintaining collectors. Costs associated with servicing and maintaining collectors will vary greatly between individual operators, and no attempt has been made to estimate these here. Here we consider only the cost efficiency of individual collectors rather than the entire collection operation. Our estimates are based on the cost of materials required to build collectors, and are applied at the level of individual collectors by dividing number of pueruli caught on a collector by the materials cost for that collector (Table 2.1).

2.2.5 Escape during hauling

This experiment was designed to test if pueruli were lost from mesh collectors in the process of hauling to the surface, and further sought to determine the stage of hauling at which losses, if any, occurred. If significant losses were detected, the possibility of changing servicing methods or collector designs could be investigated.

Twenty four mesh collectors were deployed in July 1999 to allow 3 months conditioning prior to servicing from September 1999 to January 2000. Collectors were deployed in the same fashion as for other trials in this study. A storm in early September resulted in

Table 2.1 Material costs of collector designs (AU$ circa 1999).

Collector type	Cost (AU$)
Floating crevice	140
Floating crevice with carpet	160
Standard crevice	120
Mesh	*30
Bottlebrush	20
Sandwich	120

***Cost of mesh collector reduces to AU$<10 if internal mesh is salvaged from discarded fishing nets**

the loss of 5 collectors, and the loss of mesh from a further 3. Accordingly, the size of mooring ropes was increased and the clip system on cages was altered. After these modifications no further losses were experienced, despite further heavy weather. As collectors were already conditioned by this time, it was not possible to replace lost collectors, and replication of treatments was reduced accordingly.

At each monthly sampling, 5 collectors were hauled without bagging, 5 were bagged by divers on the sea floor, and 5 were bagged after being hauled through the water column, but prior to being lifted onto the boat. Treatments were randomly assigned to mooring positions on each occasion to avoid confounding effects caused by collector interactions. Catches from September were excluded from analysis, as they would likely have included lobsters that had settled during the initial conditioning period.

2.2.6 Statistical analysis

Data from design trials and bagging trials were analysed by 2-way ANOVA, with treatment type and month considered fixed factors. Month was considered fixed as maximum puerulus settlement occurs annually in a discrete peak, usually lasting 3-4 months. In all cases, log transformation was necessary to accommodate distribution assumptions of ANOVA. A type III sums of squares model was used to accommodate imbalance caused by the loss of collectors during trials. Post hoc pairwise comparisons were conducted using the Ryan-Einot-Gabriel-Welsch range (REGWQ) test, which controls the overall experiment-wise error rate.

2.3 Results

2.3.1 Stage 1: Material selection

Thirty-two of 98 surveys were returned, and of these 8 reported no puerulus settlement. Respondents reported highest rates of puerulus settlement on 3 materials, *viz.* oyster cages (14), mussel ropes (4) and the predator exclusion cages deployed around Atlantic salmon grow-out pens (4). Small numbers of pueruli were

frequently observed on heavily fouled weights and anchors used for various purposes on marine farms.

Three locations with relatively high settlement rates were identified from survey returns and these were used in substratum studies.

2.3.2 Stage 2: Comparisons of materials

Only collectors at Great Oyster Bay caught sufficient pueruli for robust analysis. No pueruli were captured at Garden Island, while only 6 were captured at Port Arthur. Even at Great Oyster Bay, settlement was low compared with the numbers reported by oyster farmers in the survey. Eighty-one pueruli were caught from 64 ladder lifts, and the maximum catch from one ladder was five pueruli.

Catch rates varied significantly between materials (two-way ANOVA: $F_{3,48} = 2.94$, $P = 0.042$, no interaction; Fig. 2.4), with small-mesh catching significantly more pueruli than large-mesh. All other paired comparisons were non-significant. Oyster shell collectors were considered unsuitable for further development, as collectors were substantially heavier, and correspondingly harder to handle than other types, and took longer to service.

When servicing onion bag collectors, we noted that in many instances the onion bag mesh was sitting flat against the outer cage mesh. A method of preventing this and retaining some structure in the onion bag mesh would provide more suitable refugia for pueruli.

While not the focus of this trial, we note that catch rates of individual collector baskets was strongly influenced by position on ladders. Collectors on the lowest rung yielded 55.6% of the catch, and the lower 2 rungs yielded 84.0% of the total.

2.3.3 Stage 3: Collector trials

2.3.3.1 Trial 1

Crevice collectors with carpet substratum rapidly filled with sand and flotation became inadequate. They were too heavy to service

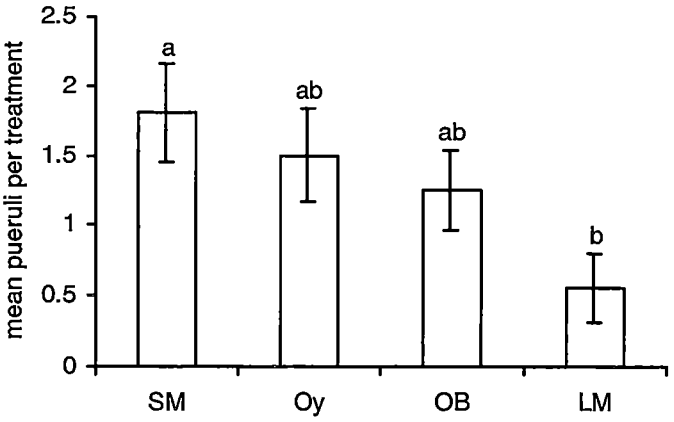

Fig. 2.4 Mean catches per ladder (±SE) by collector type (SM=small mesh, Oy=oyster shells, OB=onion bag, LM=large mesh) in substratum trials. Homogeneous subset groupings (a,b) are per REGWQ post-hoc tests.

safely using available equipment and were removed from the trial after the first month of sampling. Mesh collectors caught most pueruli in 4 of 6 months, however comparisons between catches from all collector types were not significant across all months (two-way ANOVA: $F_{2,78}$=2.0, P=0.154, no interaction; Fig. 2.5a) nor across the 3 months of highest settlement ($F_{2,36} = 2.42$, $P = 0.103$, no interaction).

Cost-effectiveness varied significantly between collector types (two-way ANOVA: $F_{2,78} = 10.2$, $P < 0.001$, no interaction), with mesh collectors proving more cost-effective than floating crevice collectors. No other comparisons or interaction terms were significant. During the 3 months of highest settlement (yielding 78.5% of the catch), cost-effectiveness of mesh collectors was significantly higher than floating crevice or standard crevice collectors ($F_{2,36} = 10.7$, $P < 0.001$, no interaction; Fig. 2.5b).

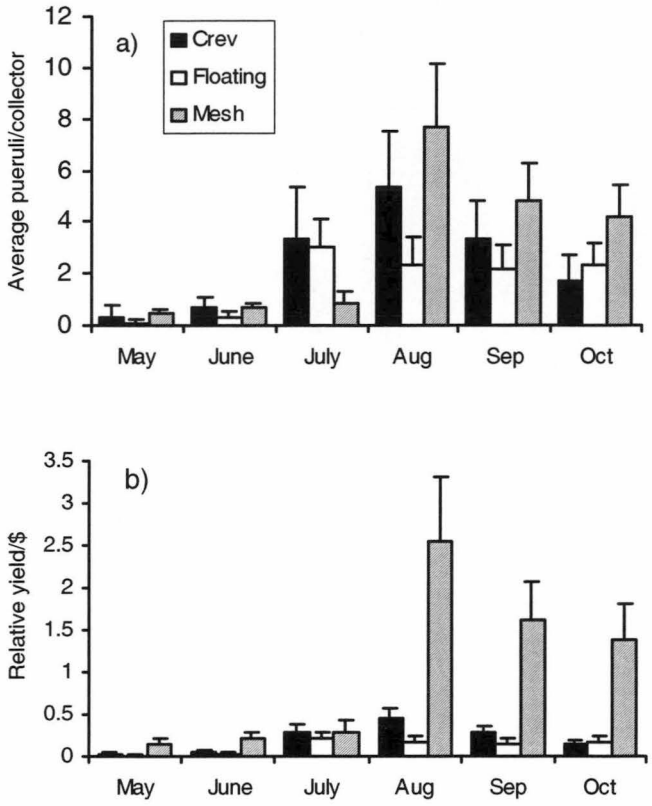

Fig. 2.5 Comparisons of a) mean pueruli per collector (±SE) for standard crevice, floating crevice and mesh collectors and b) cost-effectiveness.

2.3.3.2 Trial 2

Despite relatively low puerulus settlement during the sampling period, significant differences in catch rates were detected (two-way ANOVA: $F_{2,98} = 3.82$, $P = 0.025$, no interaction; Fig. 2.6a). Catch rates from sandwich collectors were significantly higher than from other collector types. No other collector comparisons or collector x month interactions were significant. There were no significant differences in cost-effectiveness across all months (two-way ANOVA: $F_{2,98} = 0.581$, $P = 0.561$, no interaction; Fig. 2.6b), however for the three months of highest catches (78.8% of total catch) bottlebrush collectors were significantly more cost-effective than the other collector types ($F_{2,57} = 4.121$, $P = 0.021$, no interaction).

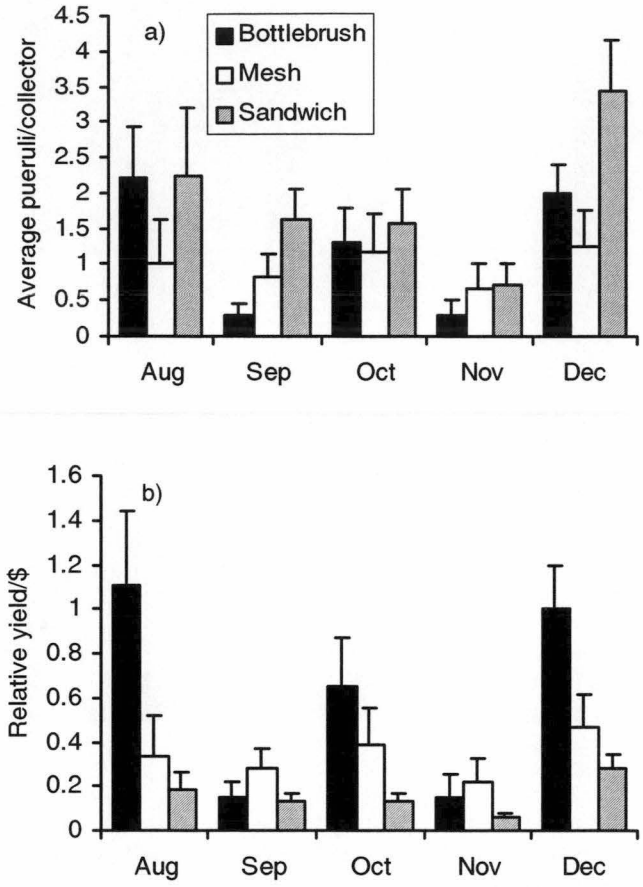

Fig. 2.6 Comparisons of a) mean pueruli per collector (±SE) for bottlebrush, mesh and sandwich collectors and b) cost-effectiveness.

Conditioning appeared less important for sandwich collectors than for other designs. When collectors were serviced in July following 3 months conditioning, catches from sandwich collectors were an order of magnitude higher than from mesh collectors, and significantly higher than from bottlebrush collectors (two-way ANOVA: $F_{2,26} = 13.1$, $P < 0.001$, no interaction; Fig. 2.7). Mean stage of pueruli from sandwich collectors was significantly higher than from other collectors for the July sample ($F_{2,26} = 4.116$, $P = 0.020$, no interaction; Table 2.2), suggesting that pueruli had settled on sandwich collectors soon after deployment and remained in the collectors. During monthly sampling the situation was

reversed, with mean stage from bottlebrush collectors being higher than from sandwich collectors ($F_{2,98} = 3.612$, $P = 0.0320$, no interaction). This implies that once conditioned, retention of pueruli on bottlebrush collectors is greater than that for sandwich collectors.

Fig. 2.7 Mean catch of pueruli per collector (±SE) following 3 months of conditioning when collectors were not serviced.

Table 2.2 Mean stage of pueruli (±SE) for the conditioning period and monthly sampling. Homogeneous subsets (per REGWQ tests) are underlined.

	Sandwich	**Mesh**	**Bottlebrush**
Conditioning	3.36±0.11	2.75±0.26	2.33±0.88
Monthly	3.16±0.12	3.23±0.18	3.56±0.08

2.3.4 Escape during hauling

Sampling for this trial appears to have coincided with a period of strong settlement, as catches from mesh collectors were higher than seen in other trials. There were no significant differences between catches from collectors bagged at the seafloor, at the sea surface, or left unbagged (two-way ANOVA: $F_{2,37} = 0.605$, $P = 0.552$, no interaction; Fig. 2.8). Power to detect differences was low (0.24) due to high variability between months, suggesting that factors other than bagging had a greater influence on catch variability.

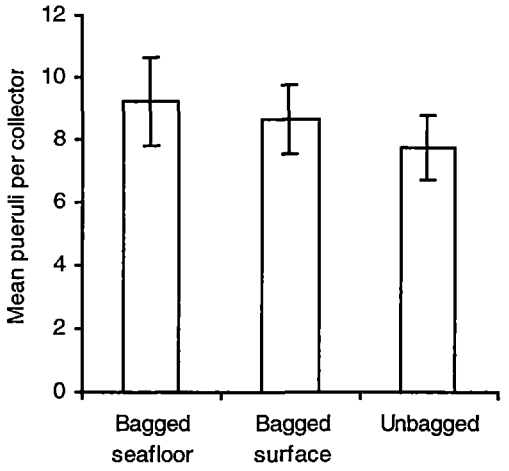

Fig. 2.8 Mean catches (± SE) for collectors bagged at the seafloor, bagged at the surface or unbagged.

2.4 Discussion

2.4.1 Collector comparisons

Puerulus settlement rates observed during these trials, as well as during routine settlement monitoring operations in Tasmania (Gardner et al. 2001), are lower than in some other areas where commercial puerulus collection is being considered such as Western Australia (Phillips 1986) and New Zealand (Booth et al. 1991). While it remains to be tested if commercial puerulus collection can be viable in these areas, low catch rates on individual collectors emphasises the need for robust, low-cost collectors that can be deployed in large numbers and serviced rapidly and efficiently.

We have shown that collectors built from cheap, lightweight materials may be more cost-effective in commercial operations than collector designs currently used in scientific studies of *J. edwardsii* puerulus settlement. Bottlebrush collectors and mesh collectors (after strengthening) proved robust and easy to handle. Being lightweight, they can be adapted to long-line deployment, and can be serviced from small vessels without the need for heavy lifting

equipment. While bottlebrush collectors were the most cost effective, cost calculations for mesh collectors were based on the purchase of new trawl netting. If netting was sourced cheaply from derelict fishing nets, cost-efficiency of mesh collectors would increase substantially.

Cost-effectiveness calculations would likely vary from those presented here if economies of scale and costs of servicing and maintaining collectors in a commercial operation were considered. These costs will be specific to individual operators and will depend on factors such as the type and size of equipment already available. Where a new operation is being established, or where, as in Tasmania, small vessels with limited lifting capacity are already in use by prospective operators, cost-effectiveness estimates presented here will be of use. Collectors with high material costs in this study were invariably the most complicated to construct and were several times heavier than collectors built from cheap materials. This would lead to higher labour costs for construction, as well as a requirement for heavier and more expensive mooring and lifting equipment, further reducing the cost-effectiveness of these collectors. Cost-effectiveness will also depend on longevity of collectors, however longer-term trials will be required to obtain this data.

Sandwich collectors caught more pueruli than other collector types in trial 2, and by inference would likely catch more than designs in trial 1. This may be explained in part by the larger size of sandwich collectors (Phillips et al. 2001), however past trials of 'seaweed type' collectors with *J. edwardsii* pueruli (Booth 1979, Kennedy et al. 1991) have also shown moderate to good catch rates. That sandwich collectors are 4 to 5 times more expensive to build and are substantially heavier than mesh or bottlebrush collectors makes them less suitable for commercial use. Heavy collectors require heavy and expensive ground tackle and will be correspondingly more expensive to service.

In both collector trials, differences in catch rates were more apparent in the 3 months with highest settlement. Likewise, Phillips et al. (2001) found that variability masked collector

differences when settlement was low. High temporal variability in settlement will be a major issue for commercial collection, as it requires that collectors must be in the water for long periods to increase the chance of coinciding with settlement peaks. That sandwich collectors require shorter conditioning times is therefore worthy of further investigation. If collectors can be deployed at short notice during settlement peaks, wear on collectors and rigging and the probability of losing collectors due to extreme weather events will be reduced.

Much of the expense of sandwich collectors is in the PVC sheets and the application of fibre tassels to these sheets. Cheaper and lighter methods of presenting fibre tassels should be investigated. This is clearly not a simple task, as one such attempt (the 'Rossbach collector', Phillips et al. 2001) resulted in significantly reduced catches of *Panulirus cygnus* pueruli, when compared with sandwich or mesh collectors. A further possibility is to alternate shade cloth 'rosettes' and layers of fibre tassels in a bottlebrush collector to combine the benefits of rapid conditioning of fibre tassels with the cost effectiveness, lightweight and apparent higher retention on shade cloth. Industry trials of such collectors have shown considerable promise (M Ether, Jolly Roger Exports, Tasmania, pers comm).

We have shown that *J. edwardsii* pueruli will settle on a diverse range of materials. While naturally settling onto rocky reef and associated macro-algal communities (Kensler 1967, Booth & Bowring 1988), they readily settle into the fine filamentous tassels of sandwich collectors, designed to mimic the seagrass habitat into which *P. cygnus* pueruli settle (Phillips 1972). Similarly, the spaces provided within the netting of a mesh collector have little in common with a rocky reef, yet have proven to be suitable for puerulus settlement. The most cost-effective option for established marine farmers diversifying into lobster culture may therefore be to look for disused materials appropriate for use in collectors available within their industry, and conduct trials against a 'control' collector known to catch pueruli. Examples of appropriate materials for recycling in this way may include course bio-filter elements, frayed rope, or various types of mesh and netting. A

basket structure similar to that used in mesh collectors is a versatile unit for comparing potential collection materials.

2.4.2 Escape from collectors during hauling

We were unable to detect differences in catches from mesh collectors bagged on the sea floor, at the surface or left unbagged. The response of pueruli to disturbance of collectors appears to be to grasp the material rather than to let go. This is consistent with the findings of Booth et al. (1991) who used diver observations to confirm that no pueruli were lost as crevice collectors were hauled to the surface. This is encouraging for commercial collection, as the expense and complication of bagging collectors can be avoided.

Chapter 3

Acoustic tracking of wild and naïve lobsters released to coastal reef

Chapter 3 has been removed for copyright or proprietary reasons.

This Chapter previously published as:

Mills DJ, Gardner C, Ibbott S (2004) Behaviour of ongrown juvenile spiny lobsters, Jasus edwardsii after reseeding to a coastal reef in Tasmania, Australia. In: Leber KM, Kitada S, Blackenship HL, Svåsand T (eds) Stock Enhancement and Sea Ranching: Developments, Pitfalls and Opportunities. Blackwell Scientific, London, p 168-180

Chapter 4

A remote multi-camera system for observing lobster behaviour and predator interactions

This Chapter previously published as:

Mills DJ, Verdouw G, Frusher S (2005) A remote multi-camera system for in situ observations of behaviour and predator/prey interactions of marine benthic macrofauna. NZ J Mar Freshw Res 39:347-352

Abstract

There are few options for obtaining information on intra and inter-species behavioural interactions between marine animals other than direct observation. Underwater video and infrared lighting can be used to overcome some of the biases and limitations associated with diver observations. We outline the assembly and application of a multi-camera underwater video system consisting largely of moderately priced components produced for the security surveillance industry. Signals from up to eight cameras on the seafloor are processed on a floating pontoon into a single video stream and transmitted to a remote monitoring station for viewing or recording. High-red and infrared lights are used for night viewing to minimise disturbance. Experiments incorporating this system have provided high-quality data on predation and behaviour of lobsters.

Keywords: Underwater video, animal behaviour, predator/prey interactions

4.1 Introduction

With the building emphasis on multi-species and ecosystem-based management of fisheries (Constable 2001), behaviour and interactions at the level of individuals have been increasingly recognised as key issues in understanding ecosystem function, organisation and response to perturbation (Piraino et al. 2002, Butler 2003). Models capable of capturing the dynamics of individuals within a system (e.g. Werner et al. 2001, Butler 2003) depend on data collected at a resolution only attainable through direct observation.

Direct observations of marine animal behaviour are restricted to varying degrees by the harsh operating environment. Physiological limits to dive duration and physical limits to range of visibility complicate such studies underwater. Behaviour of animals being observed is likely to be altered by the close proximity of divers (e.g. Rutecki et al. 1983). These difficulties are compounded when observing animals such as lobsters that are most active at night (Mills et al. 2004). Not only does diving become more hazardous, animals are also likely to respond to the presence of visible light required for observation.

Underwater video, time-lapse recording technology and lighting at wavelengths invisible to animals have been adopted to overcome these problems. The use of single camera, fixed video systems has enabled constant monitoring of a limited area for periods of hours to days (Chapman & Howard 1979, Burrows et al. 1999, Jury et al. 2001). While the use of video overcomes many of the problems and biases associated with diver observations, a single, fixed camera has a limited field of view. This problem is compounded at night when field of view is further limited by lighting. Possibilities to overcome this limitation include the use of remotely controlled cameras with zoom, pan and tilt functions, or the use of multiple cameras. We chose to adopt the latter as we believe it offers a simple, robust system with greater versatility. This paper provides details of a multi-camera system constructed predominantly using off-the-shelf items designed for the security surveillance industry.

4.2 System assembly

The camera system has three main component types: an underwater system consisting of cameras and lights; a surface pontoon system including power supply, video processor and transmitter; and a remote monitoring system including video receiver, decoder and a recording device (Fig. 4.1).

Cameras were low light (0.05 lux) black and white 1/3" CCD (charge couple device) image sensors with a 3.6 mm lens (GoVideo 3619 modules) providing a 42° viewing angle in water. Black and white CCDs were used as they have a broader wavelength detection capability than colour modules, enabling viewing with infrared light. Camera modules were protected in waterproof housings, and linked to the surface system by 30 m polyurethane-sheathed copper cable. To guarantee a clean power supply for the cameras, a switch- mode DC-DC converter (Cosel ZUS151212) was fitted providing regulated 12v DC.

We constructed high-red lights emitting a wavelength of 680 nm and infrared lights with wavelength of 845 nm for use in different circumstances. Choice of wavelength of lighting sources is critical. Absorption of light in water increases dramatically as wavelength increases into the red region of the visible spectrum, and then increases exponentially at infrared wavelengths. Increases are particularly marked at about 700 nm for red light and 850 nm for infrared light (Kirk 1994). Applying formulae presented in Kirk (1994) we find that in water, 72% of 680 nm high-red light is transmitted at a distance of 1 m and this reduces to 14% at infrared wavelengths of 845 nm.

All lights consisted of an array of 40 high-intensity light emitting diodes (max. radiant intensity ca. 120 mW/sr @100 mA) encapsulated in resin for protection and waterproofing, and connected to the pontoon system via 30 m polyurethane-sheathed cable. Two of these lights were deployed with each camera and together were capable of effectively illuminating an area of seafloor not greater than 0.8 x 0.8 m from a distance of approximately 0.8 m.

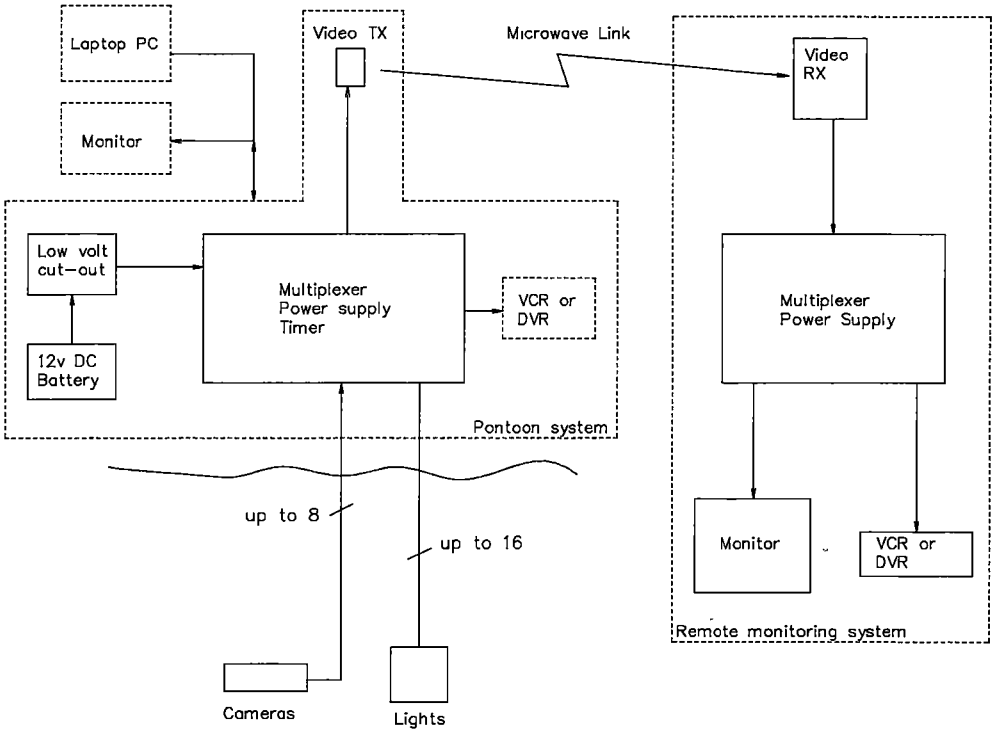

Fig. 4.1 Schematic representation of camera system. The pontoon system provides power to lights and cameras, and receives the signals from up to eight cameras. These are processed into a single data stream, and transmitted (TX) to the remote video receiver (RX). Camera settings and frame rates can be altered using a computer via a physical connection to the multiplexer unit. The multiplexed video signal can be recorded to a single storage medium (e.g. video cassette) at a remote station or on the pontoon.

Camera and light cables are connected on the surface pontoon to a weatherproof housing (Fig. 4.2A) containing the camera power supply, a timer to allow lights to be switched on and off when appropriate, and a multiplexer. A duplex time-division multiplexer (AND MPC8DX) is central to the functioning of this system. The multiplexer receives the signals from up to eight cameras simultaneously, samples the video inputs from each camera sequentially, and interleaves sampled frames into one composite video signal. This coded signal from all cameras can then be recorded directly on a single recording medium, or transmitted to a

remote monitoring station. To view the signal, whether live or from videotape, a decoding multiplexer reassembles the frames into single camera video streams. Images can be viewed with several cameras displayed on a split screen, or a single camera can be viewed in full-screen resolution. The penalty for using a multiplexed signal is that the frame rate from each camera is reduced to a degree defined by the number of cameras being monitored. For example, when recording 24 hrs of footage to a 3 hr videotape with eight cameras connected, a frame is captured from each camera at approximately 1 second intervals. Multiplexer settings including individual camera brightness and contrast, frame capture rate and on-screen displays can be adjusted using a laptop computer interfaced to the multiplexer via a weatherproof connector on the housing.

The camera signals are transmitted to a remote monitoring station using a microwave video link operating in the 2.4 GHz license-free band. Output power is low (10 mW) and transmission range varies greatly depending on weather, location and antenna type. With a directional parabolic antenna on the receiver, range may be up to 1.6 km. While this short transmission range was suited to our application, a system with a range in excess of 10 km could be built using a video server coupled with a wireless network hub. The remote monitoring station may be set up on a boat or on land, and consists of a video receiver, multiplexer to decode video signals, a monitor and a recording device. Camera signals can be recorded using a 12 v time-lapse VCR (e.g. Mitsubishi HS-7424EDC) or similar digital device. Where there is no convenient site to establish a remote station, the signal can be recorded on the pontoon. This system has the disadvantage that access to the pontoon is required to change recording media.

The pontoon base was constructed from three squares, one inside another, of welded polyethylene tubing (250 mm diameter, 12 mm wall thickness). The outer square has sides of 1.7 m. This provides sufficient buoyancy and stability to support the camera system and up to two people during battery changes and deployment. Cameras and lights are deployed by lowering them to the seafloor through a

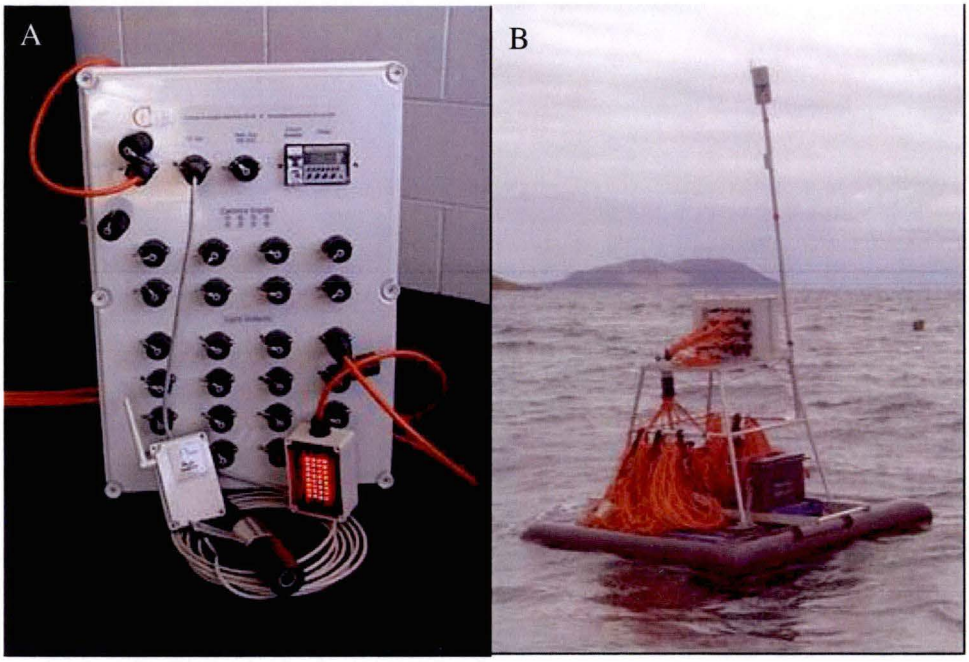

Fig. 4.2 A) Main multiplexer, power supply and timer unit with weatherproof connectors for camera inputs (eight connectors) power supply to lights (16 connectors), and multiplexer control, transmitter out and power in from batteries (one connector each). Also shown are a camera (centre front) transmitter (left front) and high-red light (lower right). B) Pontoon with light and camera cables coiled on frame ready for deployment. A moulded plastic hood covers the top of the system once deployment is complete.

0.3 x 0.3 m hole in the centre of the pontoon. An aluminium frame supports the weatherproof housing (and recording device if used) approximately 1 m above the water surface. A plastic hood (not shown in Fig. 4.2B) is placed over the housing once the system is deployed. The pontoon is held in place and stabilised by three anchors connected by chain and rope to the sides of the pontoon. This prevents the pontoon from turning and tangling the camera and light cables. The system can be deployed by three operators in a vessel as small as 7 m. Operators should consider the potential navigational hazard presented by the pontoon, and provide navigation lighting as prescribed by local regulations.

This system has the capacity to generate immense quantities of video data. For review purposes, a video signal splitter was built that enabled the signal to be fed to two multiplexers, and thus up to eight cameras could be viewed simultaneously on two split screens. When an event of interest occurred, single cameras were brought up in full screen view for detailed observation. Signals recorded in 24 hr time-lapse were reviewed at standard video speed, thus taking a minimum of 3 hours to review 24 hours of footage from up to eight cameras.

4.3 System Applications

Using this system we have observed and quantified behaviours and interactions between lobsters and predators that were previously unknown and difficult to observe by other methods. Oliver et al. (2005) monitored the fate of tethered lobsters, identifying major predators (Fig. 4.3a) and determining survival time and diel variations in predation rates. These same data were used to test the validity of tethering trials in determining spatial variability in survival rates (Gardner et al. 2004), and showed that without detailed information on predator suite composition tethering results could be very misleading. Lobster catch rates in traps are routinely used as a measure of abundance for stock assessment purposes, and a simple linear relationship between catch and abundance is assumed. Green (2002) used this camera system to observe behaviour of lobsters in and around traps (Fig. 4.3B), and demonstrated that the trap catch was influenced by a complex mosaic of interactions prior to, during and after entering a trap with only 13% of the observed lobsters being caught. These experiments illustrate the versatility of the multi-camera approach, using the cameras to observe simultaneous experimental replicates (Oliver et al. 2005), or to build a composite picture of a larger area with images from several perspectives (Green 2002).

Different lighting sources were used in the two experiments. Green (2002) was interested in lobster behaviour and interactions between lobsters. The anatomy of *Jasus edwardsii* eyes is such that they are

incapable of perceiving red light of wavelength greater than 600 nm (Meyer-Rochow & Tiang 1984). Accordingly high-red lights were used without concerns about influencing behaviour. As the extinction of high-red light in water is substantially lower than that of infrared light (Kirk 1994), high-red lights provide brighter illumination than infrared lights for the same power consumption. Oliver et al. (2005) were interested in the behaviour of lobster predators including fish and octopus. The complex eyes of these predators can likely perceive high-red light, so infrared lights were used.

The versatility of this system will see it used in the near future in diverse projects observing octopus behaviour around lobster pots, predation on invading sea urchins, comparative behaviour of lobsters on natural and artificial reef, and spawning behaviour in reef fishes. We believe that the use of video systems as described in this paper will become an integral component of research to address questions relating to ecosystem-based management and the effects of fishing on the marine environment.

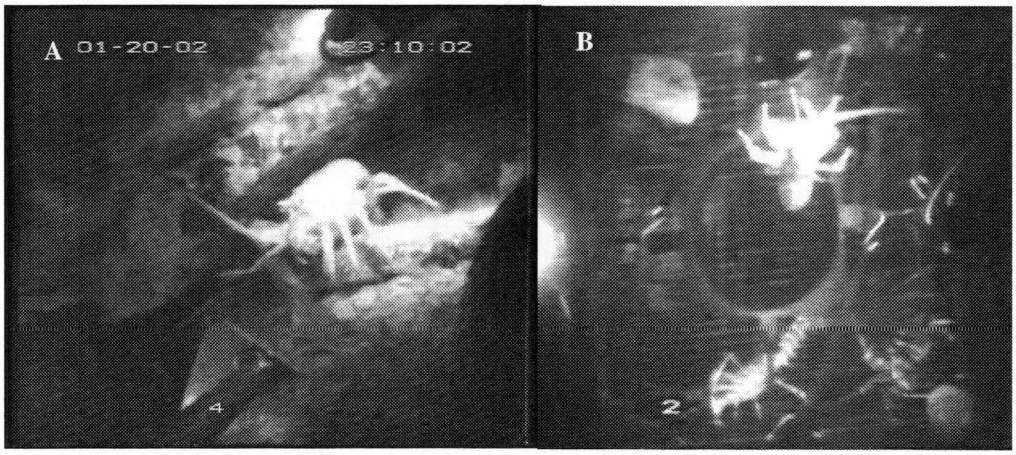

Fig. 4.3 A) Adult wild lobster observed at night under infrared light just after capturing a small tethered lobster. B) Lobster trap viewed from above at night using high-red light. One lobster is exiting the pot, while several other lobsters can be seen within the pot.

Chapter 5

Accounting for bias in tethering experiments used to select low predation sites for the release of juvenile lobsters

This Chapter prepared for submission to Marine Ecology Progress Series as:

Mills DJ, Johnson CR, Gardner C. Accounting for bias in tethering experiments used to select low predation sites for the release of juvenile lobsters

Abstract

Juvenile spiny lobsters (*Jasus edwardsii*), on-grown for 1 year from wild-caught pueruli, are released to coastal reef in Tasmania, Australia, to offset possible stock depletion resulting from the harvest of pueruli for commercial culture. Here we assess the utility of tethering experiments for selecting sites with low predation pressure appropriate for lobster releases, and address a concern that experimental artefacts are likely to vary across sites, providing biased estimates of relative mortality. A multi-camera surveillance system used to observe tethered juvenile lobsters at four isolated reefs revealed a low-diversity of predators including wrasse (45% of observed predation events), octopus (21%), crabs (17%) and large lobsters (16%). Wrasse and octopus were the dominant predators at three of the four sites, while crabs and large lobsters dominated the fourth. Survival rates measured in 48 h tethering trials varied (24.4 - 62.2%) between sites (ANOVA: $F_{3,8}$=5.404, P=0.025). The effect of tethering on predatory success of the identified predators was assessed in a reef mesocosm. Tethers substantially increased the success rates of all predators. The magnitude of the tethering effect was similar for wrasse and octopus, while large lobsters caught relatively few untethered juvenile lobsters and crabs appeared incapable of catching untethered lobsters. Survival rates for each site were adjusted by applying a site-specific correction factor, calculated using knowledge of predator suites at each site and magnitude of tethering bias for each predator. Differences in survival between sites measured by tethering were wholly a function of tethering artefacts. Corrected survival rates did not vary between sites (ANOVA: $F_{3,8}$ = 3.48, P = 0.070). Clearly, tethering trials are appropriate as a tool for selecting release sites only if complementary data on predator assemblages and tethering artefacts are collected with sufficient rigour to enable calculating site-specific correction factors.

Keywords: Tethering artefacts, survival, predation, spiny lobster, enhancement

5.1 Introduction

The release of hatchery-reared juveniles of marine species for restocking or stock enhancement purposes frequently results in poor survival (see reviews by Blaxter 2000, Brown & Day 2002). This is most often attributed to behavioural inadequacies induced by artificial feeding regimes and sensory deprivation during rearing (Berejikian 1995, Olla et al. 1998, Svåsand et al. 1998, Castro et al. 2001). Where behaviour is unaffected or problems can be redressed by changes in hatchery practices (e.g. Brown & Smith 1998, Hossain et al. 2002), the choice of optimal release sites is of primary importance (Leber et al. 1996, Kellison et al. 2003). Release sites must be selected to provide high quality habitats affording maximum protection and minimal predation pressure. As most mortality occurs in the hours to days immediately following release (Furuta et al. 1997, Blaxter 2000, Svåsand et al. 2000, van der Meeren 2000), experimental approaches that can compare short-term relative survival between sites are of value for site selection.

Mark-recapture studies are frequently used to gauge the success of enhancement operations (Bannister et al. 1994, Agnalt et al. 1999), and tag return rates from juveniles released at multiple sites have been used to define optimal release habitats (Leber et al. 1996). However, the inability to distinguish losses due to emigration and mortality can confound mark/recapture results, and large numbers of juveniles must be available to ensure sufficient returns from multiple sites. Tethering experiments have the potential to overcome these limitations by providing accurate data on the fate of a small number of juveniles with restricted mobility, however they introduce a new set of potential pitfalls. When tethering highly mobile prey, at best mortality rates will increase substantially due to reduced effectiveness of escape responses (Zimmer-Faust et al. 1994), and at worst tethered prey may be captured by predators incapable of capturing untethered prey (Adams et al. 2004). Still more insidious is the potential for non-additive, or higher order, artefacts (Peterson & Black 1994). An example of a non-additive artefact relevant to our study is that the

affect of tethering on capture rates may vary between predators (Curran & Able 1998), so that if the relative abundance of predators varies between sites, tethering results may be more a reflection of the nature of predator assemblages at particular sites than a measure of relative predation rates. Following spirited debate in the scientific literature (Peterson & Black 1994, Aronson & Heck 1995, Kneib & Scheele 2000, Aronson et al. 2001), more recently backed by substantial empirical evidence, it is now widely acknowledged that tethering experiments must be accompanied by rigorous tests of associated artefacts. This is particularly important for highly mobile prey that manifest rapid and/or unpredictable movements in effecting escape from predators. Key to robust interpretation of tethering data is information on the identity of predators (Peterson & Black 1994, Micheli 1996), behaviour of tethered prey (Barbeau & Scheibling 1994, Curran & Able 1998) and predation mechanisms (Zimmer-faust et al. 1994, Adams et al. 2004). Here we report an experiment using novel techniques to quantify and account for artefacts associated with tethering juvenile *Jasus edwardsii* (southern rock lobsters) on spatially isolated rocky reefs.

Aquaculture of *J. edwardsii* in Tasmania, Australia is progressing through the on-growing of pueruli (first benthic post-larval stage) captured from the wild. Concerns that this harvest may harm wild lobster stocks are being addressed through reseeding. This involves on-growing harvested pueruli in tanks or seacages for one year, then releasing back to the area of capture a proportion estimated to be equivalent to the number that would have survived naturally. This system of management is underpinned by a large discrepancy in natural mortality (95-97%; Herrnkind & Butler 1994, Edmunds 1995) and captive mortality (5-15%; Phillips et al. 1983, Kington 1999, Crear et al. 2003) so that, following reseeding, a large proportion of juveniles are still available for on-growing in captivity to a marketable product. The success of management by reseeding is contingent on a high survival of released juveniles.

Field and laboratory observations have shown that behaviours relating to predator avoidance, shelter use and feeding of released

on-grown juvenile *J. edwardsii* are largely indistinguishable from those of wild juveniles (Mills et al. 2004, Mills et al. in press, Oliver et al. in press). Accordingly, identification of suitable release sites prior to commercial-scale releases became a priority. While mark-recapture trials (Mills et al. in press) provide evidence of equivalent survival among on-grown and wild juveniles across multiple sites, they failed to provide a measure of relative predation rates between sites because of site-specific emigration rates. The present study assesses the potential of tethering experiments to indicate spatial variability in relative predation, employing a multi-camera surveillance system to observe predator/prey interactions in the wild, and mesocosm experiments to quantify artefacts.

5.2 Materials and Methods

5.2.1 Study sites

Because juvenile *Jasus edwardsii* are being released in southeast Tasmania as a licence requirement associated with the harvest of puerulus, we selected representative areas of accessible reef in this region (Fig. 5.1). We did not target sites with obvious variability in habitat characteristics, but rather restricted our choice to areas we judged to be suitable for lobster release. Sites were selected based on the presence of wild juvenile lobsters, an obvious abundance of appropriate sized shelter (Edmunds 1995), moderate to high macro-algal abundance to provide cover for released lobsters and accessibility for deploying camera equipment and performing regular dive surveys.

Our site in the southern corner of Adventure Bay (147°21'28"S, 43°21'254"E) consisted of a small area (ca. 60 m x 25 m) of high profile reef in 7 – 9 m water depth. Patchy low-profile reef continued for another 50 - 80 m to the north to a depth of 13 - 14 m. This site is exposed directly to ocean swell from the east, and frequent strong northwesterly winds, and there is a fetch of approximately 40 km to the NE. The biota of this reef reflects a relatively high-energy environment. Glenvar Reef (43°00'11"S, 147°23'46"E) is a discrete area of medium-profile reef (maximum

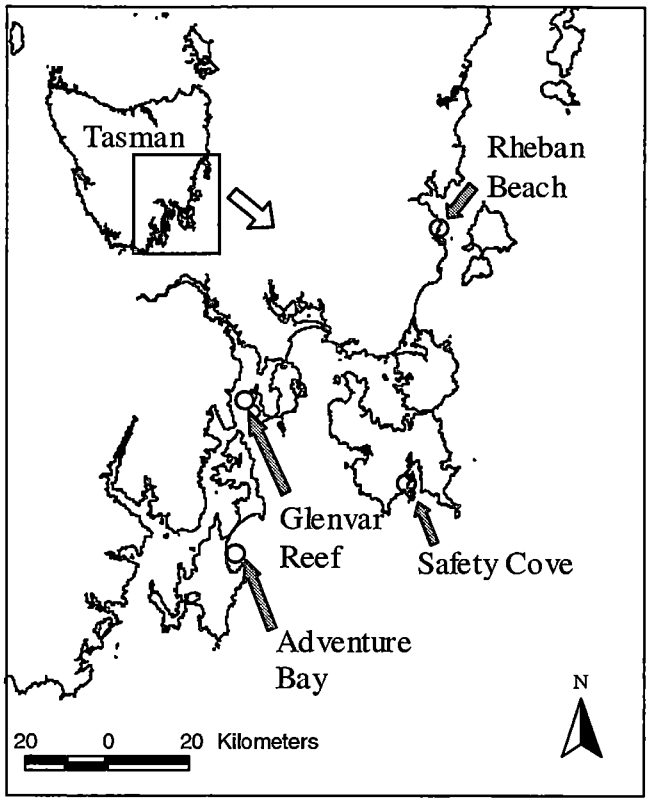

Fig. 5.1 Location of tethering sites in southeastern Tasmania.

rise 2 m) in 5 - 7 m of water in a relatively sheltered estuary, and is ca. 100m offshore from a rocky headland. There are further areas of patch reef ca.100 m to the west and shelving reef extends some 800 m south along the shoreline. Although fetch at the Safety Cove site (147°51'45"S, 43°11'5"E) does not exceed 3 km (to the northeast) the site receives considerable reflected swell from the adjacent cliffs to the east in southerly conditions. Accordingly the fish assemblage at Safety Cove is more typical of high exposure habitat than would be expected given the limited fetch (Jordan et al. 1998). The tethering site in the northern corner of Safety Cove was on an area of patch reef measuring ca. 150 m by 80 m. Rheban Point (42°36'57"S, 147°56'28"E) was the deepest of the sites (11 to 13 m) and the reef covered an area of ca. 100 m by 50 m. Extensive areas of sand and unstructured rock platform separated

this site from adjacent fringing reef. This site was moderately exposed, with a maximum fetch of ca. 40 km to the north east.

5.2.2 Experimental animals

Lobsters for tethering trials were captured as pueruli in crevice collectors (Booth & Taring 1986) deployed off southern and eastern Tasmania (Gardner et al. 2001), and on-grown in conditions similar to those of a commercial grow-out facility. Lobsters were grown in fibreglass tanks supplied with flow-through (ca. 250 lh^{-1}) water at ambient temperatures (11 to 19°C) and held at densities as high as 200 m^{-3} for pueruli, reducing to ca. 60 m^{-3} for 1 year old juveniles. Lobsters were fed daily on fresh, opened blue mussels (*Mytlius edulis planulatus*) or commercial prawn pellets, and attained sizes of 28 - 37 mm carapace length (CL) after 12 months. Lobsters for field tethering and mesocosm trials were selected haphazardly from tanks, avoiding the largest and smallest individuals.

5.2.3 Tethering and deployment

Tethering techniques were refined using tank trials until we were confident that escape from tethers was highly unlikely. On the day prior to field experiments, lobsters were 'saddled' for tethering. After drying the lobster carapace with compressed air, a short length of 6 kg breaking strain nylon monofilament was tied around the lobster between the 2nd and 3rd pair of walking legs, and a small fishing swivel with a snap-hook tied at the dorsal centre of the carapace using this line. The knot and swivel were secured with a drop of cyanoacrylate glue, and the lobsters remained in air for ca. 5 minutes to allow the glue to reach partial-cure. Recovery to apparently normal behaviour was rapid after lobsters were returned to water. The snap-hook allowed the tether to be attached to lobsters by divers in the field and the swivel minimised the likelihood of the tether becoming tangled. Each lobster was identified by a number printed on waterproof paper, which was glued to the dorsal carapace surface using cyanoacrylate glue.

In the field, lobsters were tethered to 200 g cylindrical lead weights using a 250 mm length of 6 kg breaking strain nylon monofilament. This length of tether permitted lobsters to move in and out of

hides while minimising entanglement and retaining lobsters within the field of view of cameras. Lead weights had protruding galvanised wire hooks to allow them to be secured in rock crevices.

At each tethering site, a 30 m weighted transect line marked in 0.5 m increments provided a spatial reference to determine lobster positions. Lobsters were deployed within 4 m either side of the transect line at spacings of not less than 3 m from each other. Lobsters were placed within crevices and holes in the reef judged by divers to provide good shelter from predation. Occasionally, individual macroalgal stipes were removed from the range of the tethered lobster where divers identified a risk of entanglement. We aimed to deploy 15 tethered lobsters per replicate trial, although on two occasions (one at Rheban Point, one at Safety Cove), sample size was reduced to 14 due to a lobster escaping during the deployment process. At each site, three replicate trials were performed, the transect line being moved to a different area on the reef for each trial. Ideally, the order of replicates would have been randomised between sites, however this was not feasible within the project budget due to the time taken to deploy the camera system. In all trials lobsters were deployed within 1 h of dusk.

Dive surveys were conducted 24 and 48 h post deployment and surviving lobsters then recovered. During each survey, the presence or absence of each lobster was noted, along with any evidence of lobster remains. This evidence has previously been used to identify predators responsible for individual kills (Micheli 1996), and we wished to assess the robustness of such evidence using video surveillance. Differences in tethering mortality rates between sites were examined by one-way ANOVA, with site treated as a random factor. Errors were stabilised where necessary by appropriate transformation, as indicated by a plot of means versus standard deviations.

5.2.4 Remote surveillance

A time-lapse video system was used to monitor six tethered lobsters simultaneously throughout the 48 h tethering trials. The system comprised six cameras paired with 12 infrared (IR) lights

(845 nm wavelength) connected to a surface pontoon which provided power and capacity to process and transmit video signals (Mills et al. in press). The use of IR light for night surveillance allowed observation free from biases associated with the use of visible light. Camera signals were either transmitted to the remote monitoring station via a microwave video link, or, where no suitable monitoring station could be established, recorded directly on the pontoon. Time-lapse recording resulted in a frame rate of ca. 1 frame s^{-1} for each camera.

Once the tethered lobsters were in place, divers positioned each camera and pair of lights to provide a clear image of the area of seafloor accessible to a single tethered lobster. Due to the high absorption of IR light in water (Kirk 1994) this represents the maximum area that could be effectively illuminated by two lights. When the 24 h dive survey revealed that a lobster under a camera had been taken, that camera was moved to a surviving lobster to maximise the number of predation events recorded.

Videotapes from field trials were reviewed in the laboratory. Once a predation event was located on the tape, the identity and estimated size of the predator, time of predation, and other relevant factors such as tether entanglement, were recorded.

5.2.5 Baited underwater video surveys

An independent census of the abundance of predatory fish was conducted at each site using a baited underwater video station (Willis & Babcock 2000). This technique is efficient at sampling larger mobile fish species (Cappo et al. 2004), does not require additional dive effort, and is non-extractive and therefore did not bias nearby tethering trials. An underwater colour video camera was mounted on a tripod with an 80 cm extension arm, on which was placed a bait pot (500 ml plastic jar with numerous holes in the top and sides). A 30 m cable returned the camera signal to a 12V videocassette recorder on the research vessel. A census was conducted during each tethering replicate at the four sites. The bait pot was filled with crushed juvenile lobsters and the system lowered to the seafloor for 20 minutes. Recording commenced as

soon as the camera system reached the seafloor. Video footage was later reviewed and scored for the maximum number of fish and the maximum number of potential predatory fish seen in any single frame, and the total number of species seen in the 20 minutes of footage for each replicate. Fish were scored as potential lobster predators if they were of a species and size observed as successful predators in video-monitored tethering trials.

5.2.6 Mesocosm trials

Once the identity of predators at each site was established from monitored tethering trials, we compared the relative magnitude of tethering artefacts for each predator in mesocosm trials. A reef was constructed from natural reef rock in a large outdoor raceway tank measuring 18 m x 5 m x 2 m deep (volume 180 000 l). Rocks ranged in size from 80 mm in diameter to large slabs ca. 0.8 x 0.5 x 0.3 m, and many were heavily encrusted with algae and invertebrate communities while some supported one or more macroalgal plants. Once assembled, the reef covered an area ca. 3.5 x 2.5 m and rose a maximum of 0.8 m from the tank floor, and macroalgal abundance was at a level similar to that of natural reefs used in tethering trials. The reef provided shelter of varying morphology as seen on natural reef, including large 'dens', as well as crevices and holes suitable for habitation by individual lobsters. The mesocosm was supplied with unfiltered seawater at ambient temperature at a rate of ca. 6000 lh^{-1}.

As experiments progressed some macroalgae became detached, and heavy grazing of encrusting biota by lobsters was apparent. Accordingly, each time the reef was reassembled after a replicate trial, we replaced a small percentage of rocks, including any that had lost macroalgae, with new rocks supporting similar species and sizes of algae.

Experiments compared predation rates with different predators under two conditions: (1) a mixed population of tethered and untethered lobsters, and (2) an equivalent untethered population. Type 1 experiments approximated a tethering experiment in the wild, where tethered lobsters supplemented an existing population

at sites chosen because of the presence of resident juvenile lobsters. Type 2 experiments provided an independent measure of mortality in a wholly untethered population under identical conditions. The comparison between the two trial types directly reflects the aim of the mesocosm trials, which is to produce a correction factor allowing field-based tethering trials to be used to predict predation of released untethered lobsters. Control experiments with no predators present were conducted to quantify mortality due to uncontrolled causes such as cannibalism.

After the reef was assembled and the tank filled, a single species of predator was released into the tank and given a 48 h acclimation period in the mesocosm prior to commencing experiments. Preliminary observations using the surveillance system in the mesocosm revealed that predators became acclimated quickly, and were feeding within 24 h of release. The number of predators used in each trial reflected their abundance in the wild as interpreted from video footage. For trials with octopus and fish as predators, a single predator was used. The dominant fish predator (male *Notolabrus tetricus*) is fiercely territorial, protecting ranges of 400 - 775 m^2 (Barrett 1995), and accordingly lobsters were unlikely to be subject to attack by more than one of these fish simultaneously in the wild. For trials with adult lobsters, two lobsters of the size seen to attack juvenile lobsters (100 mm $<$ CL $<$ 105 mm) were used. Video footage from field tethering trials regularly showed several red swimmer crabs (*Nectocarcinus tuberculosis*) attacking or feeding on tethered lobsters, and accordingly four *N. tuberculosis* were used in each trial. Where practical, individual predators were used in only a single replicate trial. However, capturing octopus of the small size observed attacking tethered lobsters in the field proved difficult, and so the same octopus was used in all trials. The order of trials, including control trials, was randomised with respect to predator type.

Eighteen juvenile lobsters were released in each replicate trial, with nine of these being tethered in Type 1 trials. All lobsters were measured and sexed prior to release, and released at dusk. The duration of experiments was 4 days for Type 1 trials, and 10 days

for Type 2 trials. While equivalent durations would be preferable, we found mortality rates in Type 2 trials were too often zero after 4 days, and mortality rates in Type 1 trials were often 100% after 10 days. Mortalities of 100% are not useful results, as the time over which mortalities occurred is not known. The mesocosm reef was inspected daily by a diver, and remains of any lobsters were removed, a process that would be carried out by scavengers on natural reef.

At the completion of each replicate trial, the mesocosm was drained, predators captured, and the reef disassembled. All surviving lobsters were captured, counted and measured. The reef was reassembled in a different configuration for each replicate, effectively providing a new mesocosm environment. This was particularly critical for trials using the (same) octopus.

5.2.7 Standardisation

We used the results of mesocosm trials to calculate a standardised correction factor for the four major predators. The standardised correction factor C for predator i was calculated as:

$$C_i = \frac{M_{ui}}{M_{ti} \cdot c_{\max}}$$

where M_{ui} is the mortality of untethered lobsters in mesocosm trial Type 2, M_{ti} is the mortality of tethered lobsters in mesocosm trial Type 1, and c_{max} is highest ratio of M_{ui}:M_{ti} amongst the four predators. The inclusion of the c_{max} term provides the standardisation so that correction factors fall between one and zero.

A site-specific mortality correction factor S was then calculated for each of the four sites based on the composition of the predator assemblage at each site:

$$S_j = \sum C_i P_{ij}$$

where P_{ij} is the percentage of kills at site j attributed to predator i. The site-specific mortality correction factor is expressed as a

percentage adjustment to be applied to mortality results for site j, and provides a measure of relative predation corrected for tethering artefacts as measured in mesocosm trials.

Due to differing binomial probability distributions associated with mortality rates of tethered and untethered animals in the mesocosm trials, we were unable to directly derive errors associated with the calculation of C. Errors for the corrected mortality estimates from tethering trials in the wild were derived by applying S to the results of individual tethering replicates, then averaging these corrected results. This approach is likely to underestimate total error for corrected mortality rates at each site, and will therefore be conservative with respect to type II errors. The implications of this, and other possible approaches to estimating errors are discussed in relation to the results.

5.3 Results

5.3.1 Field tethering experiments

The pattern of differences in mortality rates between sites observed after 24 h (Fig. 5.2) was accentuated after 48 h, resulting in significant differences (ANOVA: $F_{3,8}=5.404$, $P = 0.025$).

Camera observations indicated that tethered lobsters utilised the shelters into which divers released them. Lobsters often responded when first released with rapid swimming (tail flicking), however divers were instructed to persist with replacing the lobster in the shelter until the lobster remained there. When a lobster would not settle in a chosen shelter, the lobster was moved to an alternative shelter. Once settled, behaviour patterns of tethered lobsters were consistent with those of wild lobsters. Lobsters emerged from shelters soon after dusk, moving and feeding within the range provided by the tether. Occasionally lobsters were observed pulling persistently against the tether, however this involved a continuous pull on the tether rather than rapid activity likely to attract

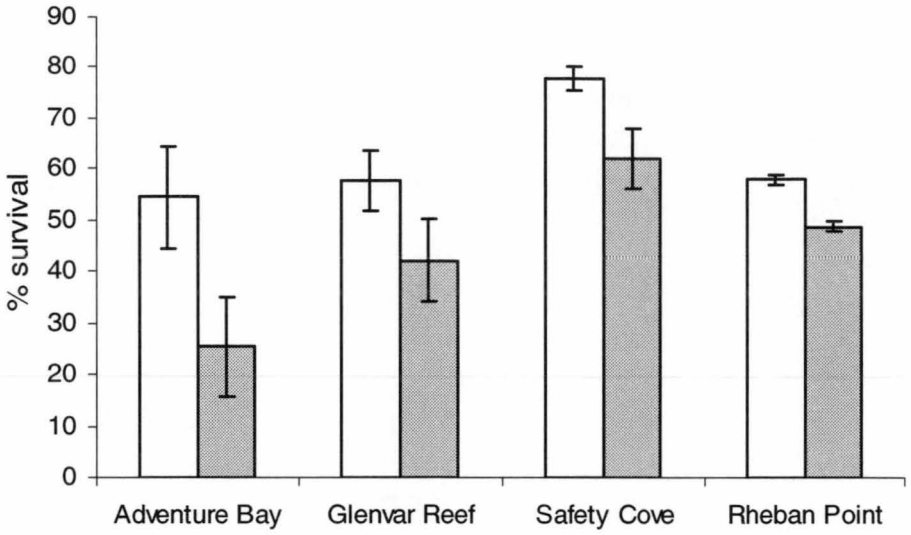

Fig. 5.2 Percent survival (±SE) from 24 h (open bars) and 48 h (shaded bars) dive surveys at tethering sites.

predators, and rarely persisted beyond a few minutes. Shelter occupancy by tethered lobsters was sporadic throughout the night, and surviving lobsters invariably returned to shelters before dawn.

Forty one predation events were recorded by the remote surveillance system. Two events were clearly the result of entanglement in camera equipment, and were not included in analyses. One predator remained unidentified, as the event occurred between camera frames. Of the remaining 38 recorded predation events, 17 (45%) were by fish, eight (21%) by octopus (*Octopus maorum*), seven (18%) by red swimmer crab (*Nectocarcinus tuberculosis*), and six (16%) were cannibalism by larger (> 80 mm CL) *J. edwardsii*. Of the fish, 12 were blue-throated wrasse (*Notolabrus tetricus*; five female, seven male), three were purple wrasse (*Notolabrus fucicola*), one was an unidentified leatherjacket (family Monacanthidae) and one kill occurred on the edge of the field of view of a camera, providing only enough evidence to identify the predator as a fish.

Successful predators were within defined size ranges. Blue-throated wrasse are site-attached protogynous hermaphrodites (Barrett 1995) exhibiting clear sexual dimorphism. A single large fish within a well defined territory becomes a male. A ratio of ca. 20 female or immature fish to one male fish of this species is typical for Tasmanian reefs (N Barrett, TAFI, pers comm). The female to male ratio of 5:7 among successful predators indicates that large size is important for predatory success with lobsters of the size tethered. Successful females were also among the largest seen on the reef. Conversely, while *Octopus maorum* can attain 1.2 m total length (TL) (Edgar 1997), only octopus estimated at 0.3 to 0.45 m TL were successful predators in this study. Octopus to 1 m TL were observed by divers at Safety Cove and Adventure Bay. All predatory red swimmer crabs were amongst the largest present on the reef (80 to 90 mm carapace width), while predatory lobsters were 80 to 110 mm CL. No lobsters larger than 110 mm were seen by divers in the areas where cannibalism was observed.

Video footage revealed that the presence of the tether directly contributed to capture in 22 of the 30 predation events where the entire capture sequence was clearly visible to a camera. Of the eight captures that did not appear to directly involve the tether, seven were attacks by fish, and one was by octopus. Attacks by fish occurred in daylight (Fig. 5.3) when lobsters were sheltering. When the tether was not directly involved, capture was the result of a direct frontal attack, and escape by the lobster was restricted by the shelter rather than by the tether. Where the tether contributed to capture, often a first 'strike' by the predator was unsuccessful, and the lobster was then pursued to the end of its tether where it was captured. Octopus attacks, which occurred at night (Fig. 5.3), were only observed on lobsters within shelters. Reasons for this are unclear. Most attacks involved the octopus disturbing the lobster through physical contact with the extremity of an arm, and then capturing the lobster as it attempted to flee. In contrast, attacks by red swimmer crab and larger lobsters occurred only when tethered lobsters were feeding away from shelter during the night. A single exception, involving predation by a lobster during the day (see Fig. 5.3), occurred when a newly

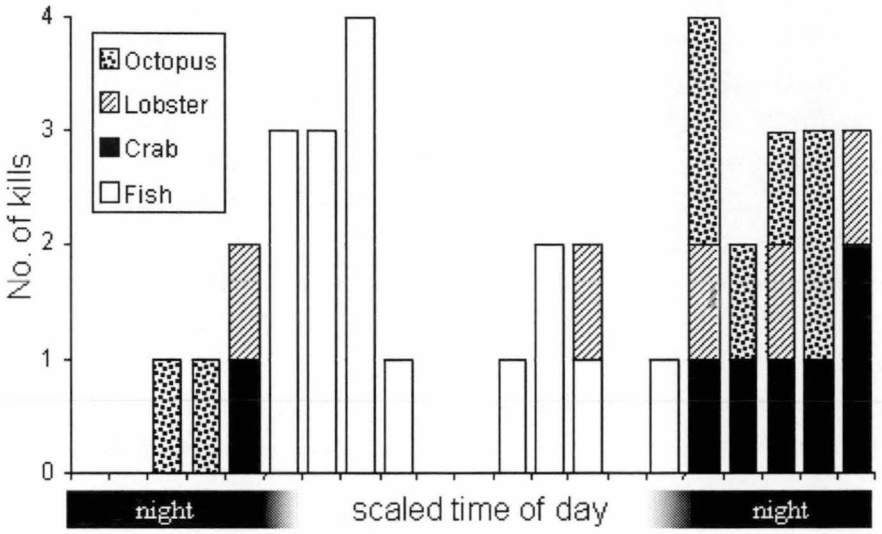

Fig. 5.3 Time of day at which predation events by different predators occurred. As trials were conducted over three months, times are re-scaled around the time of sunrise and sunset to accommodate for changing day lengths.

released tethered lobster walked into the den of a large lobster and was captured. In attacks by red swimmer crabs the tether often became entangled in the crab's chelae, and as the lobster attempted to escape, the tether became wound around the chelae, eventually resulting in capture (see video CD). Alternatively, the crab would progressively reduce the range of movement possible to the lobster by walking towards the lobster along the tether.

Two cases (one octopus, one crab) where the tether aided escape by a juvenile lobster were noted. Here, the predator attack lead to the tether anchor being dislodged from an elevated crevice. The momentum of the falling anchor was sufficient to pull the lobster from the grasp of the predator.

All but one of the predation events involved a single predator; in that instance two crabs were involved. After a successful attack by a large lobster, it was common for several red swimmer crabs to aggressively procure the prey, the lobster moving away from the kill site (see video CD).

Once a lobster was captured, octopus fed at the site of capture for the longest period, remaining unsheltered in the field of view of the camera for up to 231 minutes ($\bar{x} = 66.3 \pm 32.8$ minutes). Similarly, crabs (maximum 87 minutes, $\bar{x} = 46.7 \pm 17.9$ minutes) and lobster (maximum 30 minutes, $\bar{x} = 18.7 \pm 6.0$ minutes) tended to consume prey at the site of capture. Fish (maximum 10 minutes, $\bar{x} = 1.1 \pm 1.0$ minutes) dislodged the anchor and carried the lobster and anchor away, broke the tether, or applied sufficient pressure to pull the tethering saddle off the lobster carapace. Divers rarely found any remains at the site of lobster kills, with the exception of remnants of the carapace attached by glue to the tether. There was no correlation between the evidence remaining after a predation event and the identity of the predator. Video footage revealed that scavengers (hermit crabs, *Trizopagurus strigimanus*; red swimmer crabs, *Nectocarcinus tuberculosis*; and small shrimps, family Palaemonidae, at night, and a diverse range of small fish during the day) removed any remains after predators had finished feeding.

The composition of the predator suite varied between sites (Fig. 5.4). Of particular note is that cannibalism was only evident at Adventure Bay, and predation by crabs was also most prevalent at this site. Blue-throated wrasse were the dominant fish predator at all sites except for Glenvar Reef, where two of three predation events by fish were attributable to purple wrasse.

5.3.2 Abundance of predatory fish

The number of species observed feeding at baited underwater video stations (Fig. 5.5) varied between sites (ANOVA: F3,8= 6.485, P = 0.016), while the maximum number of fish observed in any frame was highly variable within sites, and no differences were detected between sites (ANOVA: $F_{3,8}$= 0.314, P = 0.815). It was rare to see more than two potential lobster predators in a camera frame simultaneously, and where multiple predators were present, they tended to be different species. The maximum number of predators seen in a frame did not vary significantly between sites (ANOVA: $F_{3,8}$=1.331, P = 0.331).

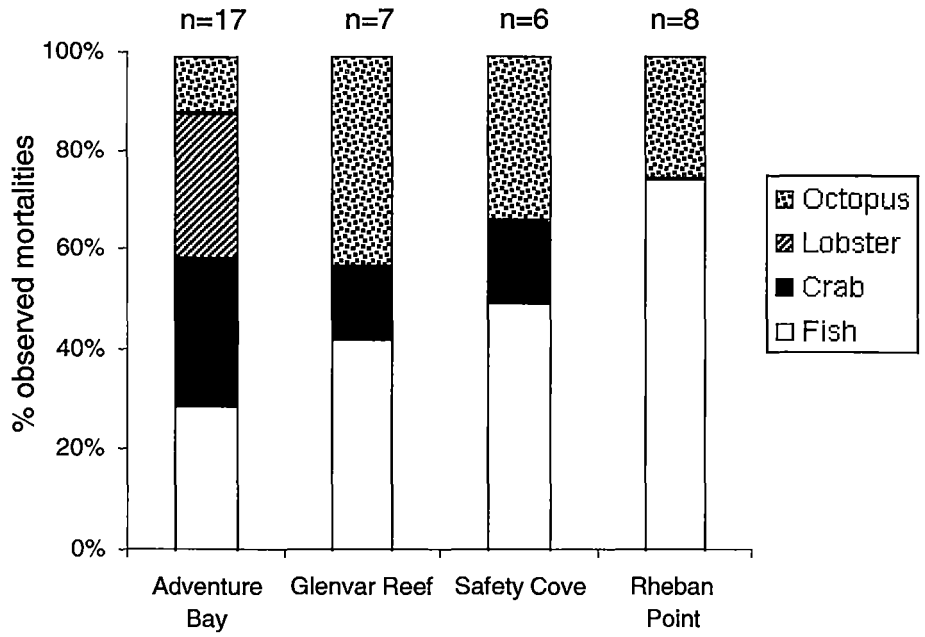

Fig. 5.4 Composition of predator suite at each site as determined by analysis of video footage from monitored tethering trials.

5.3.3 Mesocosm experiments

Rates of predation on tethered and untethered lobsters were similar for wrasse and octopus (Fig. 5.6), the two most numerous predators observed in the field trials, although both predators consumed tethered lobsters at a much higher rate than untethered lobsters. Red swimmer crab caught the highest number of tethered lobsters, but proved ineffective at capturing untethered lobsters. A single lobster from a Type 2 crab trial had one antenna and associated antennal base removed, suggesting this lobster had been captured by a crab but had escaped. Adult lobsters proved less effective than fish and octopus at catching tethered juvenile lobsters, and only a single untethered lobster was killed by a large lobster during the three Type 2 trials.

5.3.4 Standardisation

Site-specific mortality corrections produced minor changes to relative survival estimates at the three sites where fish and octopus were the predominant predators, but a major change for Adventure

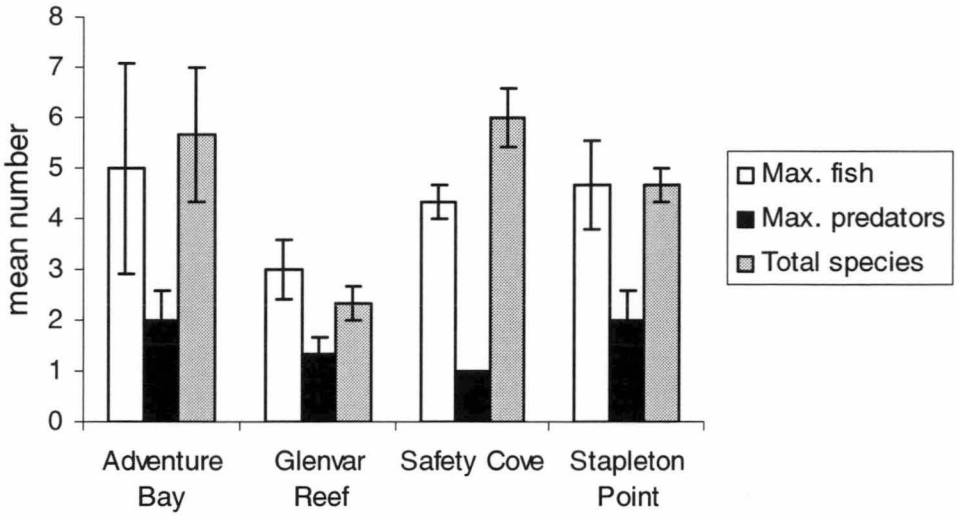

Fig. 5.5 Maximum number of fish (Max. fish) and potential predators (Max. predators) (±SE) seen simultaneously in any single frame during replicate 20 minute baited video drops at tethering sites, and the total number of fish species seen in each replicate.

Bay, where cannibalism and predation by crabs was common (Fig. 5.7). Where the magnitude of the correction was small, changes in associated errors are likely to be inconsequential. However for Adventure Bay, a reduction of over 50% in estimated relative mortality resulted in the equivalent reduction in associated error. The resulting standard error (4.94) is smaller than that predicted by the regression of standard deviations against mean for uncorrected tethering results (5.70), and considerably smaller than under an assumption of homoscedasticity of errors within sites (9.68). Despite that the likely underestimation of error terms will inflate the probability of committing a type I error, no significant difference between corrected relative survival estimates was detected (ANOVA: $F_{3,8} = 3.48$, $P = 0.070$).

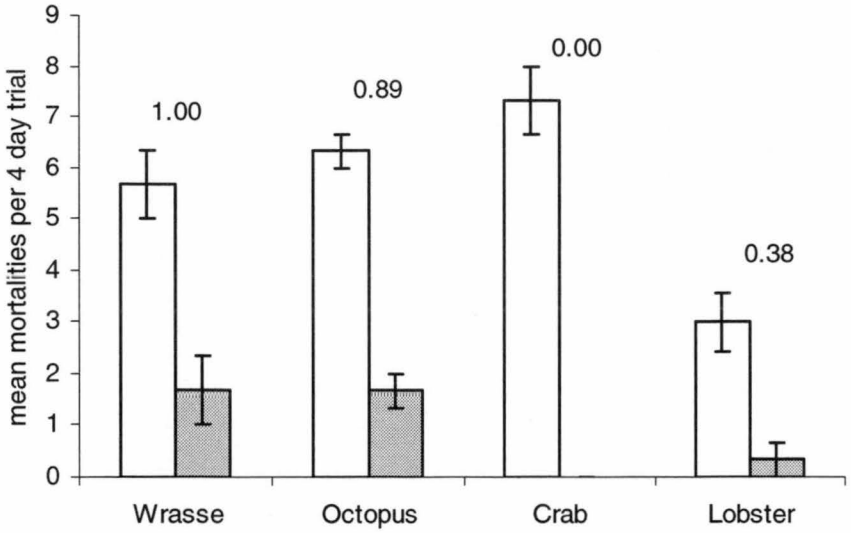

Fig. 5.6 Mean rates of mortality (±SE) for tethered lobsters from mesocosm type 1 trials (open bars) and untethered lobsters from mesocosm type 2 trials (shaded bars). Standardised species correction factors (C) from mesocosm results are shown above bars.

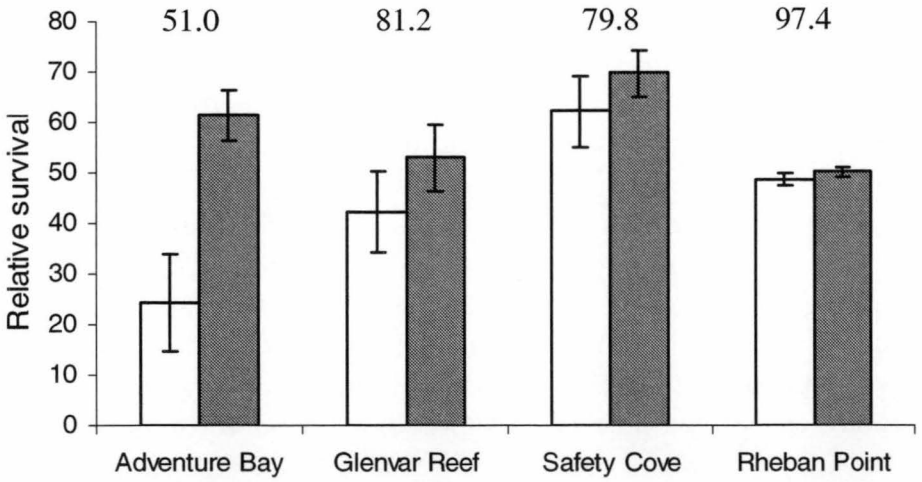

Fig. 5.7 Relative survival of tethered lobsters in the field over 48 h (open bars) and corrected values after allowing for tethering artefacts (shaded bars). Site-specific correction factors are shown above bars, and are a % correction factor applied to mortality results at each site.

5.4 Discussion

5.4.1 Predation of tethered lobsters

Vigorous discussions of the merits of tethering experiments have lead to a better understanding of the potential pitfalls of this technique and increasingly sophisticated methods of improving data quality. Chronographic tethering devices (Minello 1993, Haywood & Pendrey 1996) provide additional data on survival time, which can greatly aid the investigation of artefacts (Haywood et al. 2003). Single video cameras have been deployed to identify predators and monitor survival over periods of minutes to hours (Wahle & Steneck 1992). Our video system with the capacity to monitor multiple tethered animals over periods of several days used in combination with mesocosm experiments has provided an unprecedented level of information on the identity and behaviour of predators and behaviour of prey, ultimately facilitating meaningful interpretation of results despite predator- and site-specific artefacts.

In contrast to tethering trials with some fishes (Curran & Able 1998, Adams 2004) and crustaceans (Barshaw & Able 1990, Haywood et al. 2003), the behaviour of tethered and wild lobsters in our trials was indistinguishable. Once settled in a shelter, normal diel patterns of shelter use were assumed, and normal defensive behaviour was observed on approach by predators. Entanglement of tethers (see Adams et al. 2004) was largely eliminated by careful choice of dens and occasional removal of macroalgae. Despite the apparent absence of these artefacts identified as confounding factors in previous studies, video footage clearly showed that the preconditions for site-specific artefacts existed at our study sites. These include differences in the affect of the tether on rate of predatory success by various predators and variation in predator abundance between sites.

The lack of diversity amongst predator suites was surprising, but greatly simplified the process of quantifying and comparing tethering artefacts. The vulnerability of lobsters to predation

decreases dramatically with small increments in body size (Wahle & Steneck 1992), and clearly the size of lobsters we released excluded predation by a diverse array of smaller fish species observed by divers and baited video stations on study reefs. In addition to the observed finfish predators, we expected to see predation by a range of other species present at the sites such as conger eel (*Conger verreauxi*), red cod (*Pseudophycis bachus*) and gurnards (family Triglidae). The prevalence of crabs as a predator was unexpected, as was the high apparent rate of cannibalism. While less gregarious than larger *J. edwardsii* (Macdiarmid 1994, Edmunds 1995), wild juveniles of the size we tethered were seen to cohabit dens with large lobsters at tethering sites, suggesting that cannibalism does not play a large part in structuring wild lobster populations. The predator suite at Adventure Bay was clearly distinctive from those at other sites, with lobsters and crabs responsible for ca. 60% of predation events. Octopus and fish were the dominant predators at the other three sites, and cannibalism was absent.

While diversity at the species level was low, the four main predatory species represent three taxonomic classes (Malacostraca, Cephalopoda and Osteichthyes), each with distinct prey detection and capture methods. Variability in capture technique can lead directly to differences in the effect of the tether on the rate of predatory success (Barbeau & Scheibling 1994, Curran & Able 1998). All predation by fish occurred during daylight hours and visual detection was clearly important. Tactile detection appeared important to octopus and crabs, which were only seen feeding at night. It was unclear from the video footage how lobsters were detecting prey. Large lobsters were seen to 'pounce' on tethered juveniles from a distance, suggesting remote sensing, which is likely to be olfactory (Derby et al. 2001). Camera footage showed that the tether was directly involved in all captures by crab and lobsters, ca. 90% of captures by octopus and ca. 40% of captures by fish. It has been suggested that field-based video surveillance can provide the most complete evaluation of the tethering artefacts and variability of artefacts between sites (Peterson & Black 1994, Micheli 1996) and superficially these numbers could be taken as a

direct measure of tethering artefacts. However, there is potential for artefacts that cannot be detected or quantified visually, and for this reason we pursued an independent measure of tethering artefacts through the mesocosm experiments.

5.4.2 Quantifying the artefacts of tethering

The paradox of experimental tests for artefacts is that the tests themselves will undoubtedly induce further artefacts (Micheli 1996, Kraufvelin 1999). Quantifying the artefacts of tethering on natural reef with the full range of biotic and physical interactions present would clearly minimise the introduction of further artefacts, however if this were achievable tethering would not be required. Where the mobility of predators is considerably greater than that of their prey, the use of alternative methods for prey restraint that maintain access for predators (e.g. buried fences constraining clams; Micheli 1996), may provide evidence of the magnitude of tethering artefacts. The same cannot be achieved where both predators and prey are highly mobile. Tank trials have been widely employed to observe the effects of tethering on prey behaviour and predation rates (Barbeau & Scheibling 1994, Zimmerfaust et al. 1994, Curran & Able 1998, Kneib & Scheele 2000, Kellison et al. 2003, Haywood et al. 2003), but have been criticised for providing artificially simplified biological conditions under which to observe behaviour (Aronson et al. 2001). Clearly, in our reef mesocosm we did not attempt to recreate the diversity of biotic interactions occurring on natural reef, but rather we were concerned with replicating physical structure and direct interactions between predator and prey. This emphasis is appropriate, as the artefacts of tethering are a direct result of physical interactions involving the prey, the tether and the reef structure. We acknowledge that predators may not behave naturally due to the absence of higher order predators (Aronson et al. 2001), although we do not believe this was a significant factor in the present study. Video footage showed that fish preying on tethered lobsters were amongst the largest present on the reefs and accordingly were unlikely to be subject to frequent threat of predation. Invertebrates seen preying on tethered lobsters fed only at night, and did not appear to forage

in a risk-averse manner, often remaining exposed for long periods following the capture of tethered lobsters.

Undoubtedly the most significant artefact of tethering relates to the reduction in the effectiveness of the escape responses by prey (Barbeau & Scheibling 1994, Zimmerfaust et al. 1994). Accordingly, our objectives for the mesocosm trials were best served by maximising mesocosm size, and we assume that in the very large mesocosm we employed, the natural escape response of lobsters was not hindered. Other potential artefacts are associated with unnatural behaviour by predators due to containment, and unnatural feeding behaviour by predators or prey due to a lack of diversity of potential food items. Our Type 1 mesocosm trials, with tethered and untethered lobsters present, were designed to remove biases associated with learning behaviour in predators. Reinforcement of particular feeding behaviour through increased yield can lead to rapid improvements in efficiency of prey recognition, attack and handling in fishes (Warburton 2003 and references therein). Assuming that fish were unable to differentiate between tethered and untethered lobsters, substantial reward from successful attacks on tethered lobsters would lead to increased attacks on tethered and untethered lobsters in the wild. Given that success rate will be higher for tethered lobsters, the absence of untethered lobsters from mesocosm trials could lead to an inflated estimate of relative predation rates on tethered lobsters. Although we cannot rule out the presence of further artefacts from the use of a mesocosm, we believe that the mesocosm reef was sufficiently large and the reef sufficiently realistic to provide a meaningful relative estimate of tethering artefacts on natural reef.

The mesocosm experiments confirmed that tethering engendered a greater increase in predation rates by crab and lobster than by fish and octopus. Crabs have previously been observed 'reeling in' tethered prey (Haywood et al. 2003), while Wahle & Steneck (1992) note that crabs were particularly clumsy at handling tethered lobsters, and believed most would have escaped without the tether. Differences in outcomes from field observations and mesocosm trials confirmed the presence of artefacts that cannot be

assessed directly from video-based observations. In contrast with results obtained from experiments in the mesocosm in which effects of tethering on lobster capture were similar for octopus and fish, observations by video on natural reefs showed that the tether was involved in a much higher proportion of successful captures by octopus than by fish. Where the tether was directly implicated in a lobster capture, it is still possible that the lobster would have been captured had the tether not been present, and the probability of this will vary with predation mechanism. Foraging by octopus has been described as 'tactile and speculative' (Forsythe & Hanlon 1997), and our video footage confirms this. The response of a lobster to contact from an octopus arm was invariably to flee, which in turn triggered a high speed 'pounce' by the octopus. While lobsters were normally captured once the tether restricted movement, the speed of the octopus attack suggests that there was a high probability of capture if the tether was not present, albeit at a distance greater than the length of the tether from the point of initial contact. Attacks by fish were focused rather than speculative, and noticeably slower than those by octopus, with lobsters responding by withdrawing to shelter. Their escape was ultimately restricted by the confines of the occupied shelter rather than the tether. The suitability of shelters chosen by divers may induce further artefacts that cannot be visually assessed which would likely vary between predators employing visual or tactile detection methods.

The results of mesocosm trials, combined with knowledge of predator suites at each site, provided clear evidence that artefacts of tethering differed among sites. The magnitude of artefacts at the three sites where octopus and fish were the dominant predators was similar. The prevalence of crabs and lobsters in the predator suite at Adventure Bay resulted in a correction of over 50% to the relative mortality estimate. That differences between sites were not significant once correction factors were applied is consistent with evidence from baited video stations showing no detectable variation in the abundance of predatory fish between sites. This relates at least in part to the aggressive territorial behaviour of large blue-throated wrasse (Barrett 1996), and more generally the low

abundance of fish large enough to successfully attack lobsters of the size used in these trials. Unfortunately we do not have complementary abundance data for octopus.

5.4.3 Estimating predation rates of released naïve lobsters

The ultimate extension of our method of correcting tethering results could be to apply unstandardised correction factors from mesocosm trials (i.e. remove the c_{max} term from the equation for calculating C) directly to results of tethering trials in the wild, providing estimates of absolute predation rates in the wild. However this requires several assumptions about artefacts introduced by the mesocosm that are difficult to test. Intuitively, we would expect predation rates within a mesocosm to be high, as predators are confined with a high density of lobsters and few other prey choices. If such artefacts are distributed evenly between tethered and untethered lobsters, ratio calculations will still be applicable as conversion factors for wild tethering trials. However, given that restrictions of the escape response of tethered lobsters is the same in the wild and in the mesocosm, but escape of untethered lobsters may be limited in the mesocosm, mesocosm trials may produce an overestimate of mortality of untethered lobsters relative to that of tethered lobsters. The consequence of this would be smaller correction factors, and a corresponding overestimate of absolute mortality in the wild. Further research on the escape response of lobsters to predatory attack and distances over which predators will pursue escaping lobsters would go some way to addressing this concern. Applying the results in this way, we estimated 3.5 – 5.6% mortality for the first 48 h post-release after adjusting with the correction factors. Mills et al. (2004) released nine acoustic-tagged juvenile lobsters at Glenvar Reef of the same size as those tethered in the present study, and reported no mortalities during 11 days at liberty. This is consistent with an estimated 48 h mortality rate calculated from our tethering results for Glenvar Reef of 5.3% (±0.7% SE).

5.4.4 Are tethering trials useful for selecting release sites?

Had we accepted the unadjusted results from our tethering trials, we would have rejected Adventure Bay as a site for lobster releases

(Type I error), and favoured Safety Cove. The implications in this case are largely inconsequential beyond reducing the number of sites available for lobster release, as adjusted tethering results confirmed Safety Cove to be as suitable as the other sites we tested. However, we have shown that this outcome was entirely an artefact of the composition of predator suites at these sites. The presence of a large population of crabs or lobsters at any site would erroneously inflate estimates of relative predation rates, which might incorrectly suggest that a site with high true mortality due to high abundances of octopus and/or fish is a favourable release site. Clearly, tethering is only appropriate as a technique for selecting release sites if complementary data on predator suites and tethering artefacts are collected. While labour and equipment-intensive, the use of video-monitored tethering trials in combination with appropriate mesocosm experiments represents a way forwards for determining relative predation rates where spatial, temporal or habitat variability increase the risk of confounding by non-additive artefacts.

Chapter 6

Refining mark/recapture techniques for estimating relative survival of wild and naïve juvenile lobsters

This Chapter previously published as:

Mills DJ, Gardner C, Oliver MD (2005) Survival and movement of naïve juvenile spiny lobsters returned to the wild. J Exp Mar Biol Ecol 324:20-30

Abstract

Using multistate Arnson-Schwartz (AS) mark-recapture models, we show that naïve (captive-reared) juvenile southern rock lobsters (*Jasus edwardsii*, Hutton 1875) survived as well as wild-caught lobsters when released to an area of coastal reef. Lobsters captured as pueruli were on-grown in tanks for 12 to 18 months where they were fed to satiation in the absence of predators. Lobsters were marked with antennal tags each carrying a unique code, and released to coastal reef along with tagged wild-caught lobsters of similar size. During eight dive surveys of the release reef and three surveys of adjacent reefs over a 28 day period, divers resighted 40.3% of the naïve lobsters and 70.2% of the wild lobsters. We show that this discrepancy is a function of differing movement rates and spatial differences in resighting probability. The probability of naïve lobsters moving from the release reef to adjacent areas in the first 4 days post release (0.72 $\pm$ 0.04 SE) was almost twice that of wild-caught lobsters (0.38 $\pm$ 0.08 SE). This behavioural difference did not influence daily apparent survival (0.98 $\pm$ 0.016 SE), which was constant between groups and over time. Our results are encouraging for the potential of enhancing spiny lobster stocks by releasing juveniles, and demonstrate the utility of AS mark-recapture models as a tool for evaluating medium-term survival of mobile marine species.

Keywords: Lobster enhancement; multistate models; survival estimation

6.1 Introduction

A long history of restocking clawed lobster populations in Europe and North America (Addison & Bannister 1994, Waddy & Aiken 1998) has been supported by extensive research into the behaviour and survival of released hatchery-reared lobsters (Wahle & Steneck 1992, review by Addison & Bannister 1994, Agnalt et al. 1999, van der Meeren 2000). In contrast, restocking of spiny lobsters has received little attention (but see Herrnkind et al. 1997, Phillips & Evans 1997), largely because commercial-scale hatchery production of spiny lobster pueruli and juveniles is not currently feasible (Phillips & Kittaka 2000).

Commercial harvest of wild pueruli (first benthic post-larval stage) is being considered or trialled in several countries (Lee & Wickens 1992, Jeffs & Hooker 2000, Phillips et al. 2001, McVeigh 2002), and represents an alternative source of spiny lobsters for on-growing and release. Natural mortality of spiny lobsters during settlement and the first benthic year in the wild is thought to be high, and has been estimated at 95-97% for *Panulirus argus* (Herrnkind & Butler 1994) and *Jasus edwardsii* (Edmunds 1995). Collection and on-growing of pueruli ostensibly is a means to overcome this survival bottleneck, with mortality rates of only 5-15% being commonly reported for the first year in captivity (Phillips et al. 1983, Kington 1999, Crear et al. 2003). Hatchery-reared juvenile lobsters could be released for enhancement purposes or, alternatively, a portion of them retained for on-growing to a marketable product, with the remainder released into the wild following a year of on-growing to ensure that stocks of wild adults are not affected by puerulus harvest (see Mills et al. 2004). In either case, benefits can only be realised if survival among released lobsters is high.

The success of release programs hinges on a variety of short- (minutes to hours), medium-(days to weeks) and long-(months to years) term processes. Short-term processes include the ability of released animals to avoid immediate predation at the time of release, and can be assessed by diver or camera observation

(Howard 1983, van der Meeren 2000). Long-term processes include the ability to fully integrate with breeding populations of wild conspecifics. The development of micro-wire tagging techniques has facilitated indirect observation of these processes through fishery returns of lobsters tagged at a small size prior to release (Bannister et al. 1994, Agnalt et al. 1999). Where releases are aimed solely at fishery enhancement, these techniques provide a direct measure of success. However, if recapture rates are low there is no capacity to elucidate the underlying causes of low returns. Further, there is typically a period of several years between release and obtaining results from fishery returns.

Analytical and field methods that provide robust estimates of survival in the medium term of days to weeks (rather than years) enable an experimental approach to assess factors determining the success of release programs. Medium-term processes that may affect the survival of released juveniles include the redistribution of animals to appropriate shelter, competition for resources with conspecifics, and their ability to find appropriate food. Acoustic tracking techniques can address some issues at this temporal scale (van der Meeren 1997, Mills et al. 2004), but these studies are typically restricted to a small number of animals.

In Tasmania, Australia, licences for pilot-scale commercial harvest of pueruli have been issued with the condition that a proportion be released back to the wild after one year of on-growing. The relatively large size of these lobsters (approximately 35 mm carapace length) and preliminary knowledge of movement from acoustic tracking (Mills et al. 2004) provide a basis for the use of visible tags to assess behaviour, movement and survival in the medium-term.

Here we report on a study designed to assess survival and movement of tank-reared naïve *Jasus edwardsii* over a period of 4 weeks using mark-recapture techniques. We did not attempt to estimate absolute survival, but rather survival of naïve lobsters relative to that of wild lobsters. This approach enabled us to partition variability in survival in a biologically meaningful way.

Parallel changes in apparent survival for both naïve and wild lobsters may be indicative of either emigration, or mortality from a process affecting both groups equally (such as release technique). Divergence in apparent survival would suggest differences in the behaviour or fitness of naïve and wild lobsters.

6.2 Methods

6.2.1 Field methods

Naïve lobsters were captured as pueruli in crevice collectors deployed off southern and eastern Tasmania (Gardner et al. 2001). Lobsters were then on-grown in tanks for 12 to 15 months, attaining a size of 30 - 52 mm carapace length (CL). All tanks were fitted with hides of concrete blocks and plastic oyster mesh. Lobsters were fed daily on fresh, opened blue mussels (*Mytlius edulis planulatus*) or commercial prawn pellets. Most lobsters were held in ambient flow-through water (11 to 19°C), although a small number (<10%) were used in growth trials where water temperatures were manipulated. These lobsters were returned to ambient water at least 1 month prior to release. All lobsters were held in ambient light conditions for at least a month prior to release.

Scuba divers collected wild lobsters from the study site by hand. Despite extensive trials (Gardner et al. 2000), no effective trapping method for juvenile *J. edwardsii* has been identified. Although divers targeted lobsters in the same size range as the naïve lobsters to be released, lobsters up to 68 mm CL were collected and retained to increase the total number of wild lobsters available for release. We anticipated that larger lobsters could later be excluded from analyses if apparent survival or resighting probability proved to be size-dependant.

All lobsters were tagged with a visible tag carrying a unique colour code. Tags were made from 12 cm lengths of 0.75 mm diameter copper wire onto which was threaded up to five small coloured beads (2.5 mm diameter - black, white, blue, orange or yellow).

The wire was crimped either side of the beads to hold them in place. Black beads were used as a unique identifier for wild lobsters, and were placed first on the wire. Tag retention experiments were conducted in tanks and used to refine the application process. Tags were applied to lobsters by wrapping the copper wire tightly around the right antennal base 4 - 6 times. During tank trials lasting 30 days our tagging method had no detectable effect on mortality, moult rate or moulting success. Using this method, the only tag losses observed in trials were due to moulting. As lobsters naturally position themselves with their antennae facing the entrance of hides, divers could read antennal tag codes without disturbing the animals.

Lobsters were released on an area of patch reef adjacent to Glenvar Point (43°00'11"S, 147°23'49"E) in the Derwent River, southern Tasmania. The release reef was a discrete area of medium-profile reef (maximum rise 2 m) in 5 - 7 m of water, and was approximately 100 m offshore from Glenvar Point (Fig. 6.1). There were numerous resident juvenile lobsters. Low to moderate cover of macroalgae allowed efficient searching by divers during resighting surveys. A larger area of patchy low to medium profile reef occurred to the west of the release reef in 7 - 9 m of water. Unstructured rock platform unsuitable as lobster habitat extended along the shoreline approximately 400 m north from the release reef. Shelving reef extended some 800 m south along the shoreline, and provided good lobster habitat.

Results from acoustic tracking of wild and naïve 1-year post-settlement juvenile lobsters released at the same site (Mills et al. 2004) showed that movements of up to 144 m in a 24 h period were possible. Accordingly, searches included the release reef and all areas of lobster habitat described above.

We released 427 naïve lobsters (average CL 43.4 mm, range 30 - 52 mm) and 153 wild lobsters (average CL 48.2 mm, range 32 - 68 mm). Of the wild lobsters, 105 (69%) were within the size range of the naïve lobsters. Lobsters were transported to the release site at dusk in the 'wet well' of our research vessel, then transferred to a

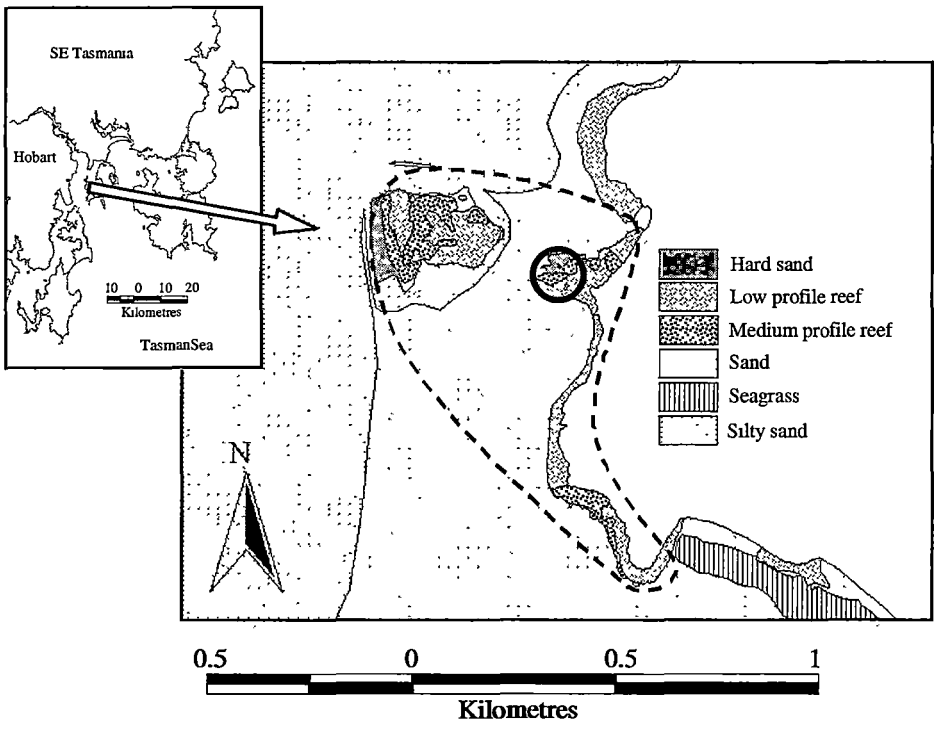

Fig. 6.1 Detail of habitat types on the release reef (within the circle) and neighbouring reef (within the dashed line) areas searched during the study.

large mesh bag for release. A diver emptied the lobsters from the bag in the centre of the reef, and did not assist lobsters in finding suitable hides or in dispersing.

Divers systematically searched the release reef on days 2, 4, 7, 9, 11, 14, 18 and 28 post-release, recording individual tag colour combinations of sighted lobsters. Due to the additional effort required to search the extensive area of neighbouring reef, these areas were searched on days 4, 18 and 28 only.

6.2.2 Modelling procedures

Model selection and data analysis methods used here were outlined by Burnham & Anderson (1998). The model selection approach seeks to identify a biologically meaningful model that best explains variability in the data, while excluding parameters that cannot be justified by the data. There is no null hypothesis or formal test of

significance, but rather the concept is one of 'best inference' given the data and a set of *a priori* models (Lebreton et al. 1992).

Resighting histories from dive surveys were analysed using Arnason-Schwartz (AS) mark-recapture models (Arnason 1973, Schwartz et al. 1993), a multistate generalisation of Cormack-Jolly-Seber (CJS) models (Cormack 1964, Jolly 1965, Seber 1965). While CJS models provide a generalised framework for maximum-likelihood estimation of apparent survival and resighting probabilities, multistate models add a further level of biological realism by incorporating movement data (Brownie et al. 1993). Models were fitted using the program MARK (White & Burnham 1999).

For naïve and wild lobsters, we estimated apparent survival probability and the probability of lobsters moving between the release reef and neighbouring reef areas in the period between consecutive surveys, and resighting probability conditional on being alive and within the sample area for each survey occasion. The fully paramaterised (saturated) AS model can be represented by $\phi(tgs)\rho(tgs)\psi(tgs)$. Thus the likelihoods of survival (ϕ), resighting (ρ) and movement (ψ) are a function of time (t), group (g = wild or naïve) and strata (s = release or neighbouring reef). Here, with eight surveys, two groups and two strata, the unconstrained saturated model has 96 parameters, namely 32 (8 x 2 x 2) parameters for each of ϕ, ρ and ψ. All models were initially structured using the identity design matrix and sin link function, as this provided meaningful estimates for the greatest number of parameters.

To confirm that the saturated model adequately described variability in the data, we followed goodness-of-fit (GOF) testing procedures set out by Pradel et al. (2003), implemented in the program U-care V2.0 (Choquet et al. 2003). While direct tests of fit for AS models are not available, this procedure involves testing for fit of a more generalised model (model JMV, Brownie et al. 1993), followed by a likelihood ratio test (LRT) between the JMV and AS models.

A series of reduced models was chosen *a priori* to test biologically and experimentally feasible hypothesis relating to factors affecting apparent survival and movement probabilities (Lebreton et al. 1992). We first imposed a series of constraints relating to experimental design and the sampling regime, removing several parameters from the model that coded no information:

1) Resighting probability on neighbouring reef was constrained to zero on days when this area was not searched;

2) Movement can only be modelled for time intervals between days on which both neighbouring and release reefs were searched. Accordingly, movement was constrained to be equal within groups for intervals between surveys of neighbouring reef; and

3) Because lobsters were released on only a single reef, movement from neighbouring reefs back to the release reef was constrained to zero for the first resighting occasion.

We then tested hypotheses relating to apparent survival and movement by sequentially eliminating parameters that did not improve model parsimony (Lebreton et al. 1992). Of a set of models, the most parsimonious model is the one that adequately describes the variability in the data with the minimum number of parameters (Burnham & Anderson 1998). Parsimony was assessed using the quasi-likelihood adjusted form of the Akaike Information Criteria ($QAIC_c$), incorporating an adjustment (variance inflation factor, $\hat{c}$) for minor lack of fit of the saturated model (Burnham et al. 1995, Anderson et al. 1998). If removal of parameters of interest for a particular hypothesis resulted in a decrease in $QAIC_c$, the hypothesis was accepted, and the reduced model was taken as the best general model against which further comparisons would be made (Burnham et al. 1995, Burnham & Anderson 1998). While this method of model selection does not allow significance values to be attributed to tests between models, normalised $QIAC_c$ weights provide a relative weight of evidence for a particular model best describing the data (Burnham & Anderson 1998).

We tested apparent survival for strata, group and time dependence, and for high mortality immediately following release. As search effort varied across time and strata, we included time and strata dependence *a priori* for resighting probability, but tested for group dependence. We tested for group dependence of movement from release to neighbouring reef and from neighbouring reef back to the release reef. Given possible group differences and an *a priori* expectation that movement would be greater in the first 24 h post release (Kington 1999, MacDiarmid et al. 1991, Mills et al. 2004), we partitioned movement on this basis, and tested for group differences for the period between release and the first survey.

To test whether apparent survival, resighting or movement of wild lobsters was influenced by size, we repeated the model reduction process, but compared models with size included as a covariate with models without the covariate. Covariate models require the use of a full design matrix and logit link function (White & Burnham 1999).

Parameter estimates were derived from the set of reduced models by model averaging using normalised $QAIC_c$ weightings, reflecting uncertainty in model selection process (Burnham & Anderson 1998).

6.3 Results

Divers recorded 624 resightings (Table 6.1) of 281 individual lobsters. Of 427 naïve lobsters released, 172 (40.3%) were resighted, while 109 of 153 wild lobsters (71.2%) were resighted. Divers located four tags on the seafloor during surveys, however due to their small size, we expect that most unattached tags would have remained undetected.

During the first night post release, lobsters remaining on the release reef redistributed to the areas providing the best refuge. These areas supported populations of resident juveniles and were heavily populated by tagged lobsters for the remainder of the study. Naïve and wild lobsters were seen cohabiting with resident juveniles. Tagged lobsters were never observed foraging away from shelters during the day.

Table 6.1 Number of resighting of wild and naïve lobsters on release and adjacent reefs for each of the eight survey occasions.

	Release reef		Adjacent reef	
Day	Wild	Naïve	Wild	Naïve
2	46	59		
4	30	32	19	28
7	30	44		
9	27	36		
11	25	24		
14	32	43		
18	22	22	5	18
28	17	17	9	39

Movement patterns by the two treatment groups differed. On the release reef, the ratio of naïve to wild lobsters changed from 2.8:1 at the time of release to 1.5:1 after 1 day. The results from searches up to 800 m from the release site during the later two dive surveys (18 and 28 days post release) showed that as distance from the release site increased, the proportion of naïve lobsters resighted by divers increased (Fig. 6.2). Beyond a distance of approximately 200 m from the release site, the proportion of naïve lobsters sighted was higher than the proportion initially released.

6.3.1 Goodness-of-fit testing

While most components of the GOF procedure indicated good fit, the LRT between the JMV and AS models for naïve lobsters was significant (χ^2= 39.48, Df = 26, p = 0.044), resulting in a significant global test for the saturated model (χ^2 = 42.65, df = 28, p = 0.038).

Contrary to the JMV model, the AS model includes the assumption that resighting probability is a first order Markov processes (Brownie et al. 1993). That is, the probability of a lobster making a transition between strata in the time interval from t to t+1 is independent of the lobster's location at time t-1. The significant LRT points to possible violations of this assumption.

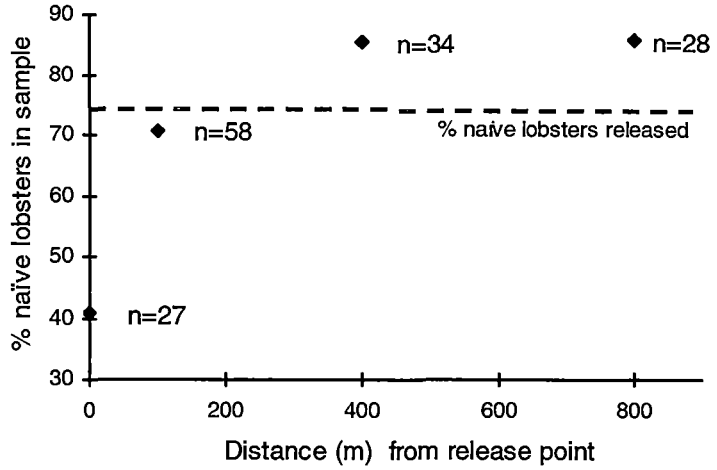

Fig. 6.2 Percentage of naïve lobsters in total tagged lobsters sighted in the last two dive surveys plotted against distance from the release point. Percentage of naïve lobsters in the initial release is shown by the dashed line.

No systematic bias was observed from individual cells within the GOF tests, and we see no underlying structural or biological reasons for the violation of Markovian assumptions. Accordingly, we report results from the full data set incorporating a variance inflator factor ($\hat{c}$) calculated from the global multistate GOF test ($\hat{c} = \chi^2/\mathrm{df} = 1.520$) (Lebreton et al. 1992, Pradel et al. 2003). A value of $\hat{c} > 1.0$ compensates for minor lack of fit by promoting models with fewer parameters, and thereby being conservative with respect to the detection of fine-scale structural features within the data.

6.3.2 Model selection

Constraints placed on the model to reflect the sampling regime reduced the number of parameters in the model from 96 to 64, while selection of the most parsimonious model reduced this further to 20 parameters (Table 6.2). Normalised $\mathrm{QAIC_c}$ weights show that the most parsimonious model $(\phi(.)\rho(ts)\Psi_1^m(g)\Psi_{2-8}^m(t)\Psi^{nr}(gt))$ is approximately eight times as well supported by the data as the next best model $(\phi(.)\rho(ts)\Psi(gts))$.

Table 6.2 Multistate model reduction process. Hypotheses and order of model reduction are given in the first column. Survival (ϕ), resighting (ρ) and movement (ψ) probabilities may be a function of group (g = wild or naïve), time (t = samples 1-8) or strata (s = release or neighbouring reef). Subscripts refer to sample occasions (1-8) while superscripts refer to strata (r=release reef, n=neighbouring reef). Model QAICc provides a measure of the parsimony of each model. Column A/R denotes whether the stated hypothesis was accepted (A) or rejected (R). Normalised QAICc weights provide a measure of the relative weight of evidence in support of a particular model, and are used for model averaging. Par shows the number of parameters estimated in the model.

Hypothesis	Model	QAICc	A/R	QAICc Weight	Par
Saturated model (with experimental constraints)	$\phi(gts)\rho(gts)\Psi(gts)$	2272.32		0.0000	64
Survival is equivalent on release and neighbouring reef	$\phi(gt)\rho(gts)\Psi(gts)$	2254.21	A	0.0000	47
Survival is equivalent for naïve and wild lobsters	$\phi(t)\rho(gts)\Psi(gts)$	2240.52	A	0.0000	40
Survival varies between groups during the initial high dispersal period	$\phi_1(g)\phi_{2-8}(.)\rho(gts)$ $\Psi(gts)$	3407.23	R	0.0000	35
Survival does not vary over time	$\phi(.)\rho(gts)\Psi(gts)$	2228.86	A	0.0001	33
Naïve and wild lobsters are equally visible on the reef	$\phi(.)\rho(ts)\Psi(gs)$	2213.51	A	0.1074	22
Probability of moving between reef areas is constant over time	$\phi(.)\rho(ts)\Psi^m(t)$ $\Psi^{nr}(gt)$	2271.54	R	0.0000	16
Probability of moving from release reef to neighbouring reef is the same for wild and naïve lobsters	$\phi(.)\rho(ts)\Psi^m(gt)$ $\Psi^{nr}(t)$	2225.28	R	0.0003	19
Probability of moving from neighbouring reef to release reef is the same for wild and naïve lobsters	$\phi(.)\rho(ts)$ $\Psi_1^m(g)\Psi_{2-8}^m(t)\Psi^{nr}(gt)$	2219.49	R	0.0054	20
Movement from the release reef differs between groups for the first time interval, and constant after this	$\phi(.)\rho(ts)$ $\Psi_1^m(g)\Psi_{2-8}^m(t)\Psi^{nr}(gt)$	2209.36	A	0.8559	20

The final model showed daily apparent survival to be constant over time, between groups and across strata, and was estimated at 0.980 ± 0.016 SE. Resighting probability did not vary between groups. Daily resighting probabilities on the release reef and neighbouring reef ranged from 0.36 ± 0.05 to 0.62 ± 0.08 and 0.03 ± 0.01 to 0.23 ± 0.13 respectively.

The probability of moving away from the release site between release and the first survey of neighbouring reef on day four was significantly greater for naïve than for wild lobsters (Fig. 6.3). In subsequent surveys there was no detectable differences between groups, and movement between strata decreased to be close to zero for the period between days 18 and 28 post release. The inclusion of lobster size as a covariate for resighting, apparent survival or movement did not improve the fit of models. Further evidence that resighting probability is independent of size is that the size frequency distributions of released and resighted wild lobsters are not significantly different (Kolmogorov-Smirnov, $\alpha = 0.01$) (Fig. 6.4).

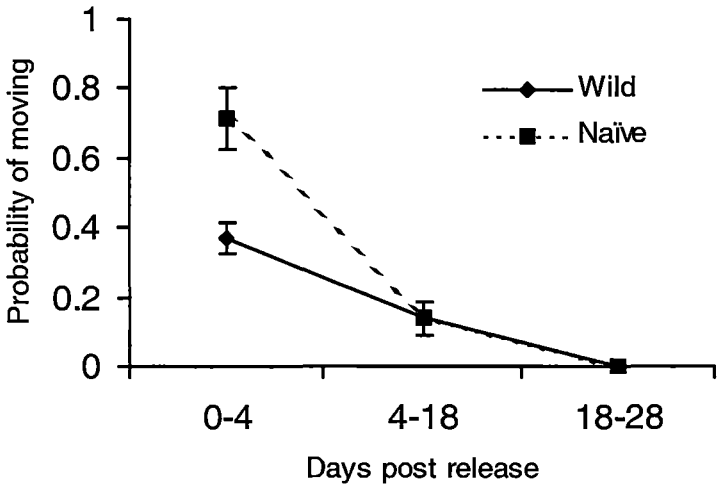

Fig. 6.3 Probability (± 1SE, adjusted for lack of fit; $\hat{c}$ =1.52) of wild and naïve lobsters moving from the release reef to neighbouring reef.

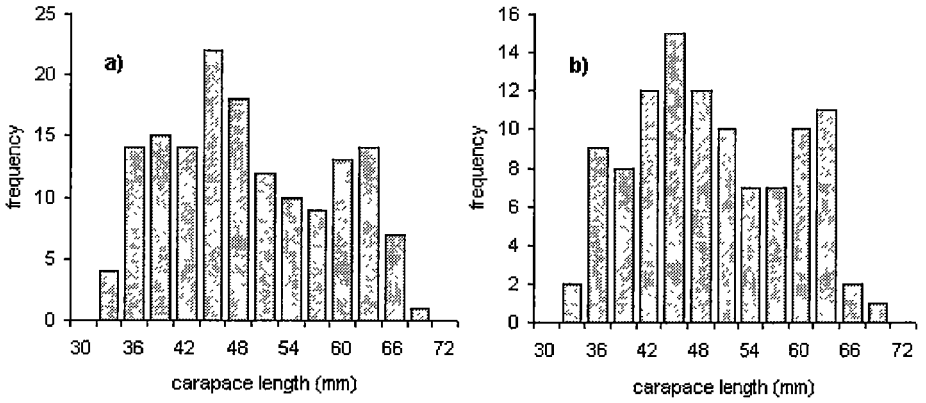

Fig. 6.4 Carapace length-frequency of released (a) and resighted (b) wild lobsters

6.4 Discussion

The versatile nature of multistate AS models makes them an ideal candidate for examining survival and movement in heterogeneous systems. Prior knowledge of likely movement of released lobsters at the study site (Mills et al. 2004) enabled us to develop an experimental design and sampling regime appropriate to meet the data requirements of multistate models. The small errors associated with the apparent survival estimate and the ability to detect differences in movement show that even with the relatively small sample sizes in this trial, tests can be powerful. Importantly, this technique has accommodated spatial heterogeneity in sampling effort where differences in reef area and habitat structure mean that standardising search effort between reef areas was impractical. Moreover, the implications of employing a less rigorous experimental and analytical regime are clear. Had we not surveyed areas of neighbouring reef in addition to the release reef, or not employed multistate models to allow for heterogeneity in resighting probability, survival of naïve lobsters would have been underestimated.

Biologically important structural features of the final model include a single parameter estimate for apparent survival, resighting

probabilities that are independent of group, and the partitioning of movement in a way that highlights behavioural differences. That apparent survival is independent of group suggests naïve lobsters are as fit as wild lobsters to survive the pressures associated with release, finding shelter and medium-term existence at the study site. Immediate exposure to predators at the time of release was not a major cause of mortality, indicated by the temporal constancy of apparent survival. This contrasts with the findings of van der Meeren (2000) who, by diver observations, estimated immediate loss during releases of clawed lobsters (*Homarus gammarus*) to be in excess of 10%. However, van der Meeren's method of release (at the sea surface) and the size of lobsters used (12 - 15 mm CL) differed from the present study where divers released larger animals (30 - 52 mm CL) on the seafloor. Apparent survival was also spatially uniform across reefs, which was expected given the proximity of, and similarities in habitat and associated predators between the release reef and neighbouring reef.

The model estimate for daily apparent survival (0.980 $\pm$ 0.016 SE) is not an absolute measure, as it may include the loss of animals due to reasons other than mortality. While searches of the neighbouring reef were extensive, it is likely that some lobsters moved beyond the area searched. Similarly, complex reef may include hides inaccessible to divers. While we do not believe this was common at the study site, any lobsters that did not emerge from such hides throughout the study would reduce the apparent survival estimate. Tank trials suggested that tag loss due to tag failure is unlikely, however tag loss due to lobsters moulting occurred in holding tanks prior to release, and undoubtedly occurred during the trial. The frequency of moulting generally peaks in *J. edwardsii* at times of highest growth, coinciding with periods of elevated water temperature (Hooker et al. 1997). Naïve animals released in this study were on-grown in tanks supplied with flow-through water drawn from the estuary in which the release trial occurred. As wild and naïve lobsters have been subject to ambient water from the same water body, it is reasonable to expect similar moulting frequencies. The four tags located on the seafloor had remnants of lobster exoskeleton attached, with no evidence of

soft tissue. While this shows that these tags did not fail, the absence of soft tissue cannot be taken as evidence that tags were lost through moulting rather than predation, as any soft tissue would have been removed rapidly by scavengers.

A breakdown in diel activity rhythms has been reported in hatchery-reared lobsters (Nagata & Koike 1997, M. Oliver unpublished data), and this is a potential threat to the survival of released naïve lobsters. Divers observed no differences in daytime shelter occupancy and activity levels in wild and naïve lobsters, and this is borne out in the lack of a group effect for resighting probability. This is consistent with research in New Zealand, which demonstrated that naïve lobsters resume nocturnal activity patterns and display appropriate anti-predator behaviour when released into the wild (M. Oliver, unpublished data).

Capture and handling of *J. edwardsii* has short-term effects on behaviour, with an increase in movement commonly reported (MacDiarmid et al. 1991, Kington 1999, Mills et al. 2004). This effect on movement was seen in both wild and naïve lobsters immediately post-release, but was more pronounced in naïve lobsters. The different rates of movement by naïve and wild juveniles suggest care must be taken in the use of wild lobsters as a control for emigration. Evidence from this study, and from acoustic tracking of juvenile lobsters at the same site (Mills et al. 2004) supports the value of wild lobsters as controls for emigration if the search area is sized appropriately. Of nine acoustic tagged wild and naïve lobsters tracked for 11 days (Mills et al. 2004), six moved further in the 24 h following release than at any other time during the study. The maximum distance moved by any lobster in the 24 h following release was 144 m, and this was the maximum displacement of any lobster from the release point throughout the study. At the completion of the study only two lobsters were further from the release point than their positions recorded 24 h after release. Distances moved declined rapidly as the study progressed, and five lobsters were recorded in the same positions from days 7 to 11. Clearly if all appropriate habitat accessible to lobsters during the initial high dispersal period is contained within

the search area, emigration from the search area will be low, and group differences in movement immediately following release will not confound survival estimates.

Higher movement probability amongst naïve lobsters immediately post-release implies longer periods away from shelter, and accordingly greater exposure to predators (Herrnkind & Butler 1986, Ball et al. 2001). However, the observed behavioural difference did not translate to a detectable difference in apparent survival. This may be a consequence of innate predator avoidance behaviour in naïve lobsters. Alternatively, it could be the product of low predation pressure at the study site. Behavioural deficiencies that would lead to mortality where predators are abundant may be inconsequential where natural predation rates are low. However, estimates of predator abundance from baited underwater video stations as well as video-monitored tethering trials (Chapter 5) suggest predation pressure at this site is equivalent to that of other coastal areas of Tasmania.

Results of this study are encouraging for the potential of enhancement of spiny lobster populations. The lack of detectable differences in apparent survival between naïve and wild lobsters and the small errors around the survival estimate provide strong evidence that the habitat at the study site is appropriate for lobster reseeding, and that robust survival estimates can be obtained from pilot-scale releases of juvenile lobsters. Further experimental releases across a range of habitat types could be conducted to correlate habitat structure with lobster survival. Importantly, our results suggest that the suitability of individual sites being considered for large-scale release could also be assessed by pilot-scale releases of visually marked juveniles.

Chapter 7

Comparing survival of wild and naïve stocks at multiple sites

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Abstract

We used mark-recapture methods to assess the relative survival of naïve and wild-caught juvenile lobsters released to coastal reef in southeast Tasmania, Australia. Naïve lobsters were captured as pueruli (first benthic post-larval stage) and reared in tanks for 12 to 18 months. Naïve and wild-caught lobsters were identified individually by an antennal tag and released by divers at four sites. In dive surveys performed over 3 to 5 weeks we resighted similar numbers of wild and naïve lobsters at two of the sites, but significantly more naïve lobsters at the remaining sites. Multistate mark-recapture models detected no difference in apparent survival between treatment groups at three of the sites. Lower apparent survival of naïve lobsters at the fourth site was attributed to the small size of this reef and the absence of adjacent lobster habitat. Many naïve lobsters did not recognise habitat boundaries and moved away from the release reef onto sand. Acoustic tracking revealed that selecting release sites with contiguous reef extending a minimum of 30 m in all directions should negate losses of this kind. At three sites apparent survival estimates were low for wild and naïve lobsters in the 24 h following release. Apparent survival was much higher when lobsters were released into seafloor cages. Acoustic tracking indicated that low apparent survival of lobsters released outside cages was due largely to emigration from our survey areas rather than losses to predation. By following simple criteria in the selection of release sites it is possible to ensure that survival rates among released naïve lobsters are equivalent to those of wild lobsters released in the same manner.

Keywords: Fishery enhancement, survival estimation, multistate models, reseeding, lobster tagging, juvenile lobsters, lobster movement

7.1 Introduction

Survival of hatchery-reared (naïve) animals released to the wild depends on morphological and behavioural attributes of released animals (review by Svåsand et al. 1998, Davis et al. 2005), appropriate choice of release sites (Gunneroed et al. 1988, Dance et al. 2003) and appropriate timing of releases (van der Meeren 2000, Oliver et al. in press). While the implications of altered behaviour and morphology can be studied in isolation in the laboratory, the effects that these characteristics have on survival once animals are released in the wild is dependent on interactions with habitats and predators. Ultimately, this can only be assessed using field-based release trials.

Due to difficulties associated with estimating true survival in the field, results from release trials are often reported as the percentage of released individuals recaptured or percentage of the catch that comprises released individuals (e.g. Kitada et al. 1992, Agnalt et al. 2004, Sakai et al. 2004). While these statistics are useful for directly gauging the effectiveness of fishery enhancement programs, where fishery returns are low they provide no mechanism to elucidate the underlying reasons for this. Ultimately, *in situ* comparisons with wild populations provide the best benchmark to test the competence of naïve juveniles for survival in the wild (e.g. Stoner & Davis 1994, Tettelbach et al. 2002, Kellison et al. 2003, Davis et al. 2005). Survival lower than that of wild juveniles clearly reduces the effectiveness of release programs, while survival greater than that of wild juveniles suggests a competitive advantage to hatchery-reared animals, increasing the risk of displacing rather than enhancing wild stocks.

Juvenile lobsters on-grown for 1 year after capture as pueruli (first benthic post-larval stage) are being released in Tasmania, Australia, as a method of maintaining wild stocks in the face of small-scale harvest of pueruli for aquaculture purposes (Mills et al. 2004). To gauge the success of this compensatory procedure, and to make informed decisions about the proportion of on-grown lobsters

that should be released, information about survival following release is required. Behavioural experiments have shown that while patterns of shelter use by naïve (on-grown) juvenile *Jasus edwardsii* held in captivity were quite distinct from those of wild lobsters, natural emergence patterns were evident when naïve lobsters were released to the wild (Gardner et al. 2005). Habitat use and emergence patterns of released juvenile *J. edwardsii* tracked using acoustic tags was indistinguishable from that of wild lobsters, and while diets of naïve juveniles varied from wild juveniles, naïve juveniles were able to find sufficient quantities of appropriate food (Mills et al. 2004). The pilot scale releases reported here represent the final extension of this behavioural research, and were conducted to assess the risk of high mortality rates associated with large-scale releases.

It is well documented that the period of greatest risk for released juveniles is the hours to days following release (Furuta et al. 1997, Blaxter 2000, Svåsand et al. 2000, van der Meeren 2000, Dance et al. 2003, D'Anna et al. 2004). Mills et al. (Chapter 6) develop field and analytical protocols for using mark/recapture trials to estimate relative survival of wild and naïve juvenile lobsters over these time scales. Here we employ these techniques to compare relative survival at four sites chosen to be representative of the habitat types and the geographic range over which commercial releases will occur. Further, we use cages and acoustic tracking to investigate movement of lobsters when first released, and we comment on the usefulness of cages as a tool for decreasing early mortality rates of released juveniles.

7.2 Materials and Methods

7.2.1 Release sites

Sites in southeastern Tasmania (Fig. 7.1) were selected based on the presence of wild juvenile lobsters, an obvious abundance of appropriate sized shelters (see Edmunds 1995), moderate to high macro-algal abundance to provide cover for released lobsters and accessibility for performing regular dive surveys.

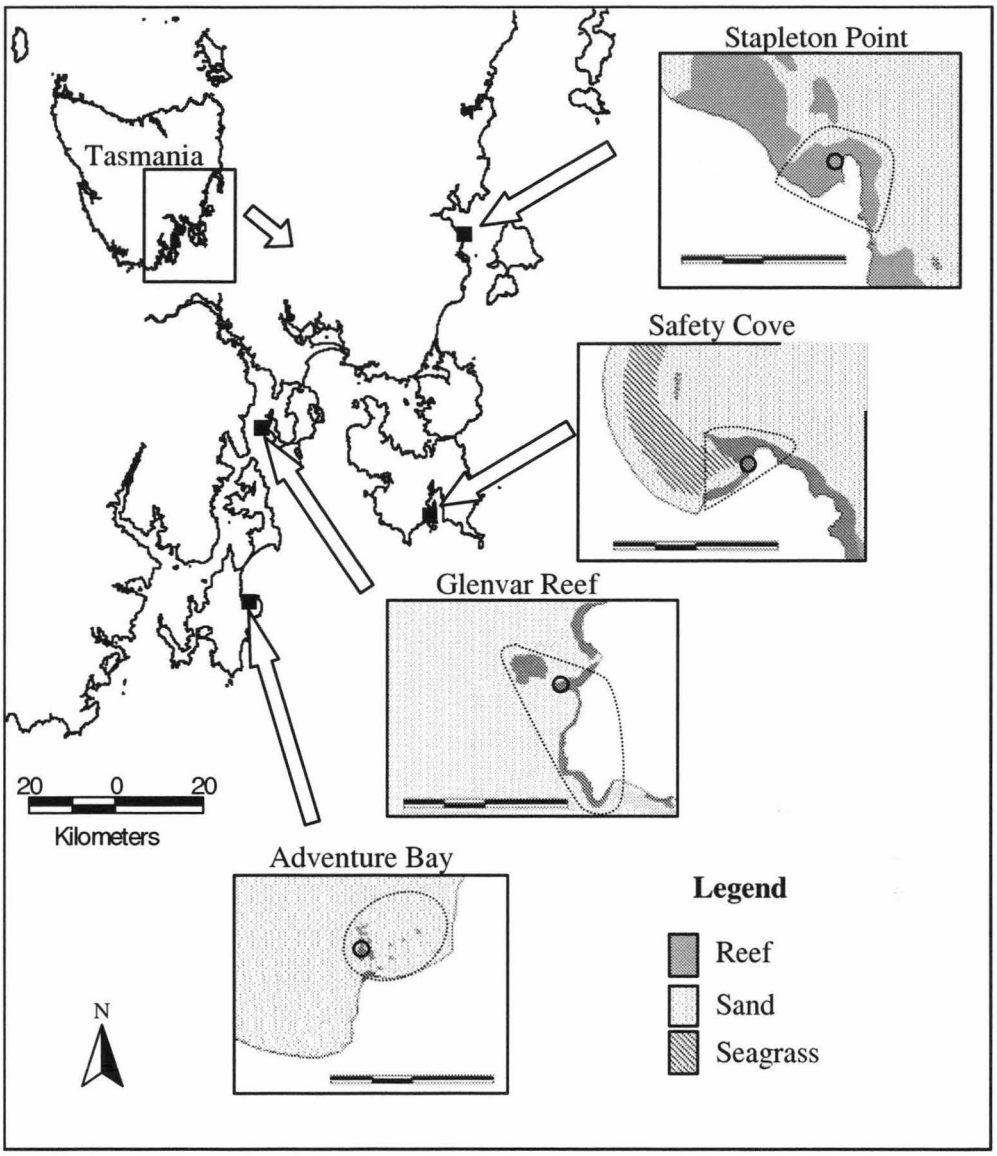


Fig. 7.1 Location of release sites in southeastern Tasmania, with inserts showing details of habitat distribution at each site (scale bar length for insert maps = 1 km). Circles on insert maps show the area of reef surveyed as the release area, while dashed lines indicate areas surveyed as adjacent reef.

The release site at Glenvar Reef (43°00'11"S, 147°23'46"E) consisted of medium-profile reef (maximum rise 2 m) in 5 - 7 m of water, connected to a rocky headland by ca. 100 m of unstructured rock platform. A larger reef ca.100 m further offshore to the west as well as shelving reef extending some 800 m south along the shoreline comprised good lobster habitat. Reef to the north of this release site was unstructured platform unsuitable as lobster habitat. Maximum fetch was ca. 8 km in southerly and southwesterly conditions, and biota were typical of moderately sheltered habitats.

Adventure Bay (147°21'28"S, 43°21'25") differed from other sites in its isolation of the release reef from other potential lobster habitats. A small area of high profile reef in 7 – 9 m water depth extended to patchy low profile reef continuing ca. 50 m north into a depth of 13 - 14 m. Sandy areas to the east were punctuated by occasional large rocks, some of which provided lobster habitat. This site was exposed directly to oceanic swells from the east, and frequent strong northwesterly winds, and there is a fetch of approximately 40 km to the NE. The biota of this reef reflects a high-energy environment.

Release sites at Safety Cove (147°51'45"S, 43°11'5"E) and Stapleton Point (147°55'43"S, 42°35'42"E) were both on large areas of fringing reef protected by headlands. However, while geographically similar, the sites differ markedly in microhabitat structure. The substratum at Safety Cove consisted of small angular boulders, providing a complex array of potential lobster shelters over much of the reef. In contrast Stapleton Point provides widely dispersed areas of good quality shelter under large boulders, interspersed by rubble fields with little interstitial space. Both sites included areas of high macroalgal standing stock, although extensive sea urchin (*Heliocidaris erythrogramma*) barrens existed in water deeper than ca. 7 m at Stapleton Point. Stapleton point experiences a small arc of exposure to oceanic swells from the NE and a maximum fetch of approximately 40 km in the same direction.

While fetch is low (maximum 3 km to the NE) at Safety cove, the site receives considerable reflected swell from adjacent cliffs in southerly conditions, and accordingly the fish assemblage at this site is reflective of high-energy environments (Jordan et al. 1998).

7.2.2 Experimental animals

Naïve lobsters for pilot scale releases were captured as pueruli (first benthic post-larval stage) of 10 to 12 mm carapace length (CL) in southern and eastern Tasmania. Some pueruli (ca. 40%) were provided by a licensed commercial operator and were obtained from predator exclusion cages around salmon culture pens during cleaning operations. The remainder were obtained from purpose-built puerulus collectors (Booth & Taring 1986, Mills & Crear 2004) deployed for research purposes.

Lobsters were on-grown in tanks for 12 to 15 months, attaining 30 - 52 mm CL. Lobsters were supplied with ambient temperature (11 to 19°C) flow-through (ca. 250 lh^{-1}) seawater and fed daily on fresh, opened blue mussels (*Mytlius edulis planulatus*) or commercial prawn pellets. Holding densities were as high as 200 m^{-3} for pueruli, reducing to ca. 60 m^{-3} for 1 year old juveniles.

SCUBA divers captured wild lobsters by hand within a week of each reseeding event. Although divers targeted lobsters in the same size range as naïve lobsters, this size of animals were rare, so wild lobsters up to 75 mm were collected to increase numbers available for release. We anticipated that larger lobsters could later be excluded from analyses if survival or resighting probability proved to be size-dependent.

7.2.3 Tagging methods

All lobsters were tagged with a visible tag carrying a unique colour code. Tags were made from 12 cm lengths of 0.75 mm diameter copper wire onto which was threaded up to five small coloured beads (2.5 mm diameter - black, white, blue, orange or yellow). The wire was crimped either side of the beads to hold them in place. Black beads were used as a unique identifier for wild lobsters, and were placed first on the wire. Tag retention

experiments were conducted in tanks and used to refine the application process. Tags were applied to lobsters by wrapping the copper wire tightly around the right antennal base 4 - 6 times. Using this method, the only tag losses observed in trials were due to moulting. As lobsters naturally position themselves with their antennae protruding from hides, divers could read antennal tag codes without disturbing the animals.

7.2.4 Releases

The number of lobsters available for each release (Table 7.1) depended on the strength of puerulus settlement 12 months previously, the mortality rate during on-growing, and the provision of lobsters from industry participants. Lobsters were transported to the release sites first by road in a 1.5 m^3 seawater tank with oxygen provided via an airstone, then in the wet-well of our research vessel. At the site lobsters were transferred to large mesh bags (ca. 200 lobsters per bag) for release by divers.

Some of the naïve lobsters were released into seafloor cages at two of the sites (Safety Cove and Stapleton Point; Table 7.1). This was to examine (1) whether providing an acclimation period on the seafloor for 48 h prior to release altered lobster behaviour in a way that increased apparent survival and (2) if by tracking acoustically tagged caged and uncaged lobsters we can determine if caging effects are due to changes in lobster movement. Cages were constructed from braided nylon mesh (25 mm stretched mesh size), covered ca. 9 m^2 of seafloor and rose 1 m above the seafloor. The base was open and the edges weighted with two chains (6 mm and 8 mm), one at the base of the cage walls, and a second on a skirt of mesh that extended approximately 50 mm beyond the cage walls. The roof of each cage was suspended with small foam floats. Once deployed, divers ensured that the chains provided a good seal with the reef, preventing the escape of lobsters and excluding predators. Lobsters were released into seafloor cages 48 h prior to uncaged lobsters being released.

At Stapleton Point six acoustically tagged naïve lobsters were released in a cage, and six were released uncaged. Acoustic tags

(Sonotronics IBT96-1) were glued to the dorsal surface of each lobster carapace using fast-setting epoxy resin. Each tag emitted a different frequency (70 - 79kHz) and a unique 3-digit pulse code to allow individual identification of lobsters. We used boat-mounted (Sonotronics DH-4 hydrophone, Sonotronics USR 5W receiver) and diver-held (Vemco VUR-96) acoustic receivers to pinpoint the position of acoustically tagged lobsters 24 h after release. The bearing from the release point was measured with a hand-bearing compass, and distance estimated from surface buoys placed at resighting locations.

Uncaged lobsters were released and cages lifted about 1 h before dusk. Divers released uncaged lobsters from mesh bags on the seafloor, and did not assist lobsters in finding shelter or dispersing.

Table 7.1 Numbers of tagged lobsters released at each site. Numbers released into seafloor cages are shown in parentheses.

Site	Naïve	Wild	Total
Adventure Bay	601	199	800
Glenvar Reef	427	153	580
Safety Cove	250 (104)	214	464
Stapleton Point	253 (96)	102	355

7.2.5 Direct observations

Divers noted lobster and predator behaviour associated with release, then retreated from the release area and continued observations for 20 - 30 minutes noting attraction of predators to the site and dispersal of lobsters from the release area. More intensive post-release observations were conducted at two sites. At Safety Cove lobsters were released at dusk (1900). Divers visually surveyed the release area at 2100, 0300 and 0600 h by performing a grid search of 30 m^2 around the release site, and noting the presence and behaviour of lobsters and predators. At Adventure Bay the release reef was monitored for 48 hr after release by six infrared capable video cameras (see Mills et al. 2004). This system

was installed 4 days prior to the lobster release, minimising disturbance to the site. Two cameras were positioned to record a broad view of the release area, and the remaining cameras were focused on large rock crevices representing important lobster shelters within the release area. Video footage was reviewed and scored for behaviour of predators and reseeded lobsters.

7.2.6 Resighting surveys

Resighting surveys were conducted by SCUBA divers in the release area and areas of adjacent reef highlighted in Fig. 7.1. At the first site (Glenvar Reef) we conducted eight surveys of the release area over 28 days (ca. 3 diver-hours per survey), however the large areas of adjacent reef were searched on only three occasions (days 4, 18 and 28 post release; 12 diver-hours per survey). Analysis of data from Glenvar Reef (Chapter 6) highlighted both the differences in movement between treatment groups in the few days following release, and the importance of data from adjacent reef areas. Accordingly at the remaining three sites the release reef and adjacent reef areas were searched on each survey occasion requiring, ca. 9 diver-hours per survey. These sites were searched daily for the first 4 days, then at increasing time intervals, ultimately up to 10 days apart. All sites were surveyed on 6-8 occasions.

We used knowledge of likely scales of movement (Chapter 3) and position of natural habitat boundaries to identify the area to be searched at each site. Transect lines up to 400 m long were laid across the search area to provide a point of reference for divers. On each survey divers equipped with a slate and a torch recorded colour codes from antennal tags of resighted lobsters, and position on the transect line to an accuracy of about 10 m. Individual divers were not assigned to the same search areas within a site on consecutive surveys, thereby reducing familiarity with lobster positions within the search area. This protocol was adopted to minimise bias in individual lobster resighting probabilities.

7.2.7 Mark-recapture analysis

We used maximum likelihood methods to estimate the conditional probability of survival, resighting and, where practicable, movement between release and adjacent reef areas for wild and naïve lobsters. Results from caging trials were analysed in a similar way, with caged and uncaged lobsters indicated as distinct treatment groups. Survival and resighting likelihoods can be estimated with Cormack-Jolly-Seber models (Cormack 1964, Jolly 1965, Seber 1965). A multistate extension of these models (Arnason 1973, Schwartz et al. 1993) provides for transitions between states, which in our case was movement between reef areas. Multistate models are of particular value in the current study as they accommodate heterogeneity in resighting probabilities between the small release area and extensive areas of adjacent reef (see Chapter 6). However, a saturated two-state (release and neighbouring reefs) model will comprise three times as many parameters as the equivalent single state model, and the small data sets in this study did not always support multistate models. Models were fitted using the program MARK (White & Burnham 1999).

We started the modelling process by testing the goodness-of-fit (GOF) of the saturated multistate model with time (t = 1 to n sample occasions), group (g = wild or naïve), and state (s = release or adjacent reef) dependence for survival (ϕ), resighting (ρ) and movement between states (ψ). We followed GOF testing procedures set out by Pradel et al. (2003), implemented in the program U-care V2.0 (Choquet et al. 2003). Where significant lack of fit is indicated, testing procedures allow for further investigation of structural problems with the data (Pradel et al. 2003). Where minor overdispersion in the data was indicated we calculated a variance inflation factor ($\hat{c}$) later used to adjust the sensitivity of the model selection process to the detection of fine-scale structural features within the data (Anderson et al. 1998). Where major violations of model assumptions were detected, or data were inadequate to test GOF, multistate models were not used.

A series of reduced models were chosen *a priori* to test biologically and experimentally feasible hypothesis relating to factors affecting

apparent survival and the likelihood of movement to adjacent reef areas (Lebreton et al. 1992). Prior research showed movement rates were likely to be high for 24 to 48 h following release (MacDiarmid et al. 1991, Mills et al. 2004), and may differ for wild and naïve lobsters (Chapter 3). Accordingly, we included models with independent and group-dependent estimates of survival and movement probabilities over this period. As search effort varied across time and strata, we included time and strata dependence *a priori* for resighting probability, but tested for group dependence. We tested for group dependence of movement from release to neighbouring reef and from neighbouring reef back to the release reef.

Models were selected through an iterative process of pairwise comparisons between the parsimony of a starting model, and that of related but simplified models from the candidate set. Parsimony was assessed using the quasi-likelihood adjusted form of the Akaike Information Criteria ($QAIC_c$), incorporating where necessary the variance inflation factor ($\hat{c}$) to allow for minor overdispersion in the data (Burnham et al. 1995, Anderson et al. 1998). If the $QAIC_c$ of the simplified model was lower than that of the starting model, the simplified model was adopted as the best general model against which further comparisons would be made (Burnham et al. 1995, Burnham & Anderson 1998). While this method of model selection does not allow significance values to be attributed to tests between models, normalised $QIAC_c$ weights provide a relative weight of evidence for a particular model best describing the data (Burnham & Anderson 1998).

Parameter estimates were derived from the set of reduced models by model averaging (Burnham & Anderson 1998). This involves calculating the average of the parameter estimates from the set of most plausible models, weighted using normalised $QAIC_c$ weightings. This procedure incorporates model selection uncertainty in the estimate of parameter precision, and thus produces unconditional estimates of variances and standard errors.

A limitation of mark-recapture models relying wholly on tag resighting data is that survival estimates (referred to as 'apparent' survival) are confounded by any event other than predation that leads to a tag becoming permanently unavailable for resighting. In our case the most likely event of this nature is permanent emigration of tagged individuals from the study area, however tag loss due to tag failure or lobsters moulting, or lobsters remaining in hides inaccessible to divers for the duration of the study will have the same effect. In this study we control for most of these factors by estimating the survival of naïve lobsters relative to that of wild lobsters. However there is potential for group differences, and independent estimates of predation mortality from tethering trials corrected for experimental artefacts (Chapter 5), and data on movement from acoustic tracking trials, aid with the interpretation of results.

7.3 Results

7.3.1 Resighting surveys

While we intended to repeat resighting surveys over ca. 30 days, rough weather resulted in durations of between 23 days (Safety Cove) and 43 days (Stapleton Point). The percentage of tagged lobsters resighted during surveys ranged from 23.2% for naïve lobsters at Safety Cove to 70.2% for wild lobsters at Glenvar Reef (Table 7.2). Low resighting rates at Safety Cove relate directly to the difficulty in searching the complex habitat present at this site. At Glenvar Reef and Adventure Bay considerably more wild lobsters than naïve lobsters were resighted, while similar percentages of the two treatment groups were resighted at Safety Cove and Stapleton Point (Table 7.2).

While searches were generally restricted to the areas defined in Fig. 7.1, incidental reports from Adventure Bay provided useful additional information. Two days after lobsters were released, a research diver resighted a tagged naïve lobster on sand ca. 400m from the release site. The lobster was alive, but unresponsive to stimuli. Two weeks after lobsters were released, recreational divers

reported sighting antennal-tagged lobsters at Grass Point (43°20'55"S, 147°22'20"E), ca. 1.9 km NNE of the release reef. We investigated this sighting, finding two wild lobsters and one naïve lobster co- habiting in a crevice at the reported position. Further searches of the area failed to find additional tagged lobsters.

Table 7.2 Results from resighting surveys at the four sites including number of surveys (duration of study in days shown in parentheses), total number of resightings reported by divers (No. resightings), number of individual lobsters resighted at least once in the survey (No. lobsters), and the percentage of the naïve and wild lobsters released that were resighted (results from caging experiments shown in parentheses).

Site	Surveys	No. resightings	No. lobsters	% naïve	% wild
Glenvar Reef	8 (30)	624	281	40.3	70.2
Adventure Bay	8 (27)	593	251	25.3	49.7
Safety cove	6 (23)	202	114	23.4 (47.0)	23.2
Stapleton Point	8 (43)	321	169	45.9 (57.3)	44.8

7.3.2 Direct observation of releases

Divers noted the attraction of small fish of several species to the activity associated with releases. These fish were invariably too small to successfully attack released lobsters, although several unsuccessful attacks were noted. Two mortalities directly associated with release were observed, one by a purple wrasse (*Notolabrus fucicola*) at Safety Cove, and one by a larger conspecific (*Jasus edwardsii*) at Adventure Bay. Divers did not observe any predator activity during night dives at Safety Cove on the night of release, although predators may have been disturbed by the diver's torchlight. Only eight tagged lobsters were observed during these dives, suggesting lobsters dispersed rapidly from the release site after dusk or moved into cryptic microhabitat at the site.

Video surveillance at Adventure Bay revealed no detectable change in predator abundance on the release reef in the 90 minutes between the lobster release and dusk, however swimming activity

by predators already present increased after release. Several potential predators (blue-throated wrasse, *Notolabrus tetricus;* purple wrasse, *Notolabrus fucicola*; six-spined leatherjacket, *Meuschenia freycineti*) were observed actively 'patrolling' the release reef. Aggressive behaviour towards other large fish by the highly territorial (Barrett, 1995) *N. tetricus* was frequent after the release. Approximately 40 min after release, a successful lobster capture by *N. tetricus* was observed on camera, although the fate of the lobster is unknown as it was alive and largely undamaged when carried beyond the field of view of cameras.

Soon after release there were 35 lobsters within the field of view of the four cameras focussed directly on crevices. Ten of these lobsters moved beyond the field of view prior to dusk. The use of infrared light enabled continued observation of crevices at night. Most of the lobsters moved out of the crevices in the 3 hours after sunset. Numbers of lobsters within the monitored crevices fluctuated throughout the night, and at dawn nine lobsters were present. During the second night post-release all lobsters left the monitored crevices, and by dawn five had returned.

7.3.3 Model selection and parameter estimation

Goodness-of-fit tests revealed minor overdispersion for most saturated models ($1.1 < \hat{c} < 1.8$), and model selection was adjusted accordingly. At Safety Cove, there were insufficient resightings of uncaged wild lobsters on adjacent reef to perform GOF tests for the multistate model. As tests showed good fit for the saturated single-state model, our starting model for Safety Cove was a single-state, time- and group-dependent model.

Differences in movement between wild and naïve lobsters were detected at Glenvar Reef, while differences in apparent survival were evident only at Adventure Bay (Fig. 7.2). At Glenvar Reef the likelihood of naïve lobsters moving from the release reef to adjacent reef in the days immediately following release (0.72 ± 0.04

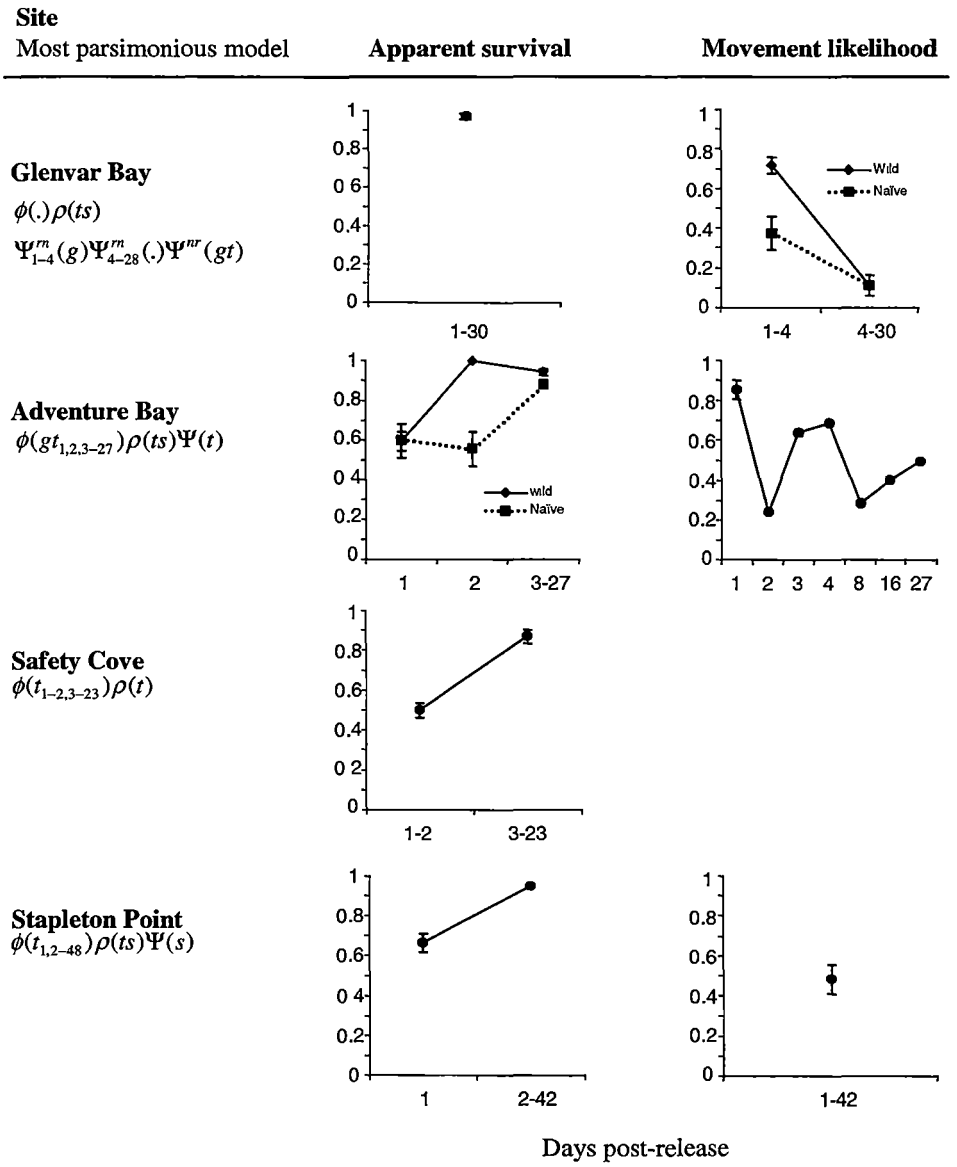


Fig. 7.2 Most parsimonious model, apparent survival estimate (±SE) and likelihood of movement to adjacent reef areas (±SE) for the four sites. Survival (ϕ), resighting (p) and movement (ψ) probabilities may be a function of group (g = wild or naïve), time (t = survey days 1 - 48) or strata (s = release or neighbouring reef). Subscripts refer to survey days (1 - 48) while superscripts refer to strata (r=release reef, n=neighbouring reef). A point (.) indicates a single parameter estimate.

SE) was almost twice that of wild lobsters (0.38 ± 0.08 SE). Apparent survival of naïve lobsters at Adventure Bay was lower than that of wild lobsters for periods between all resighting surveys except the first two, the greatest difference being observed on the second day after release. These differences were not an artefact of size differences between wild and naïve treatment groups, as models in the candidate set that included a size co-variate (CL) for resighting or survival likelihoods were not well supported.

Low apparent survival estimates for 24 to 48 h post release were common to three of the four sites (Fig. 7.2). Caging studies provided valuable data to assist in separating components of apparent survival attributable to movement or emigration.

7.3.4 The effect of releasing lobsters in cages

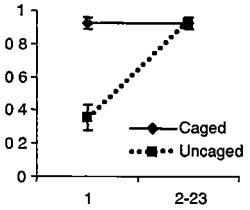
The small numbers of tagged lobsters sighted outside the release area at Safety Cove again dictated that a single state model be used at this site and, accordingly the likelihood of movement between release and adjacent reefs could not be calculated. The use of release cages had a dramatic effect on apparent survival at this site. Apparent survival of caged lobsters in the first 24 h after release, estimated by a single parameter, was high (0.92 ± 0.04), while that of uncaged lobsters over the same period was low (0.38 ± 0.05), but was equivalent to that of caged lobster thereafter (Fig. 7.3).

At Stapleton Point multistate models detected a similar caging effect, although differences in apparent survival between the two groups was smaller. Movement in the 24 h following release was clearly suppressed by the use of cages, with uncaged lobsters (0.79 ± 0.07) almost twice as likely as caged lobsters (0.42 ± 0.09) to move from the release reef to areas of adjacent reef. No differences between the two groups of lobsters were detected beyond the first resighting survey.

Site Most parsimonious model	Apparent survival	Movement likelihood

Safety Cove

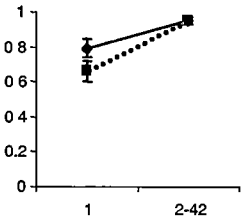
$\phi_{caged}(.)\phi_{uncaged}(t_{1,2-23})\rho(t)$

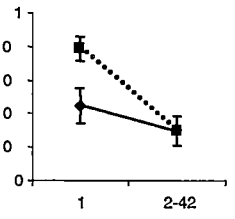


Stapleton Point

$\phi(gt_{1,2-42})\rho(ts)\Psi^{r-n}_{caged}(.)$

$\Psi^{r-n}_{uncaged}(t_{1,2-42})\Psi^{n-r}(t_{1,2-42})$





Days post-release

Fig. 7.3 Most parsimonious model and model-averaged parameter estimates for caging trials at Safety Cove and Stapleton Point.

7.3.5 Acoustic tracking

Of the six caged and six uncaged naïve lobsters released with acoustic tags, one caged lobster was never relocated after cages were lifted, and one uncaged lobster moulted within the first 24 h following release (the tag was recovered still attached to the exuviae). We do not know the fate of the lobster that was never relocated; possibilities include loss to predation, that the lobster moved beyond the area surveyed, or that the tag malfunctioned.

The remaining five lobsters from each treatment group showed conclusively that caging has a major effect on movement during the first 24 h following release (Fig. 7.4). Of the five caged lobsters, two did not move from the areas where they were caged, one moved 8 m and two moved 15 m in the 24 h after removal of the cage. Movement of 15 m coincides with the boundary between areas searched as release reef and adjacent reef. In contrast the

minimum distance moved by uncaged lobsters was 20 m, and one lobster, which moved 30 m to the north, was located outside the area searched by divers and under an isolated rock platform. Differences in movement away from the release site between the two groups of lobsters were highly significant (1-way ANOVA: $F_{1,8}= 16.98$, $P = 0.003$).

Lobsters inhabited a combination of solitary hides and larger dens with wild juveniles present. The two caged lobsters that moved 15 m NE and ENE were under opposite sides of a large flat boulder inhabited by at least 50 wild juveniles. The two uncaged lobsters that moved 20 m N were under a similar, but smaller rock while all other lobsters inhabited solitary hides.

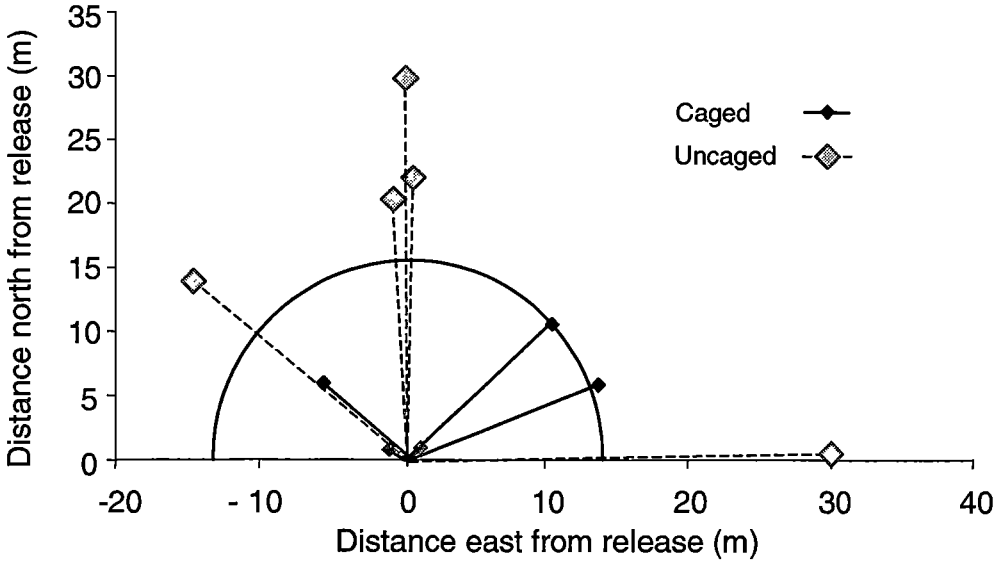


Fig.7.4 Distance and direction moved from point of release by caged and uncaged naïve lobsters during the first 24 h post-release. The semi-circle represents the approximate position of the demarcation between areas surveyed as release reef and adjacent reef.

7.4 Discussion

Final model structure for mark-recapture trials at each site is influenced by interactions between lobster behaviour, site characteristics and survey structure. Accordingly, knowledge of movement and behaviour, as well as details of habitat structure at each site, is critical to interpret model output.

7.4.1 Relative survival

At three of the four sites there was no detectable difference in apparent survival between tagged naïve and wild lobsters. At the fourth site (Adventure Bay) apparent survival was lower for naïve lobsters. While survival of released hatchery-reared juveniles has often been reported to increase with increasing body size (Bilton 1980, Masuda & Zieman 2000), the larger size of wild lobsters in this study did not account for the observed differences in survival, as inclusion of lobster carapace length as a covariate in tagging models did not significantly change estimates or improve model fit. The susceptibility of lobsters to predation decreases rapidly with small increments in CL (Wahle & Steneck 1992), and it appears that even the smallest lobsters in this study were of a size above the mortality bottleneck associated with settlement and early benthic life (Herrnkind & Butler 1994), and were able to fend off most potential predators.

Mark/recapture trials alone cannot identify the components of apparent survival that underpin the observed differences. Tethering trials corrected for experimental artefacts (Chapter 5) showed that predation rates at Adventure Bay were not significantly greater than those at other sites in the study, and so predation is unlikely to be the cause. Similarities between sites in the assemblages of predators revealed by video census and diver observations (Chapter 5) support this finding.

Comparisons with results from Glenvar Reef, the site closest to, and physically most similar to, Adventure Bay, suggest that interactions between movement and habitat structure may explain the observed differences. At both Glenvar Reef and Adventure Bay

we resighted many more wild than naïve tagged lobsters. However, at Glenvar Reef apparent survival was equivalent for the two groups. Following handling and disturbance spiny lobsters exhibit a 'flight' response lasting about 24 h, during which they move significantly greater distances than undisturbed lobsters (MacDiarmid et al. 1991, Nagata & Koike 1997, Kington 1999). During this 'flight' response, naïve lobsters at Glenvar Reef tended to move further than tagged wild lobsters (Chapter 3) and were more likely to ignore habitat boundaries, crossing sand and settling on distant reef areas (Mills et al. 2004). Due to lower search effort on distant reefs, the probability of resighting naïve lobsters at Glenvar Reef was lower than that of wild lobsters. The multistate tag/recapture model was able to account for this heterogeneity in resighting probability, producing equivalent estimates of survival for the two groups.

The release reef at Adventure Bay is largely surrounded by sand. Accordingly, the probability of lobsters encountering nearby reef within the search area during the 'flight' response period is low; to find reef in many directions would require movement over several kilometres of sand. An analogous situation to that seen at Adventure Bay can be recreated by reanalysing results from Glenvar Reef but omitting recaptures from distant reef areas. The resulting apparent survival estimates (Fig. 7.5) reflect those seen at Adventure Bay, rather than the single parameter estimate obtained for the complete dataset at Glenvar Reef.

While the differences in apparent survival appear to relate directly to movement rather than to predation, greater time away from shelter leads to greater predation risk (Herrnkind & Butler 1986, Ball et al. 2001). Nonetheless, evidence from diver reports at Adventure Bay shows that some lobsters do survive to find appropriate shelter on distant reefs, implying that mark/recapture models have overestimated mortality. However the recapture of a moribund lobster on sand 400 m from the release point shows that some lobsters were unsuccessful in finding shelter beyond the release reef. The risk associated with leaving the shelter of the release reef, transiting several kilometres of sand and ultimately

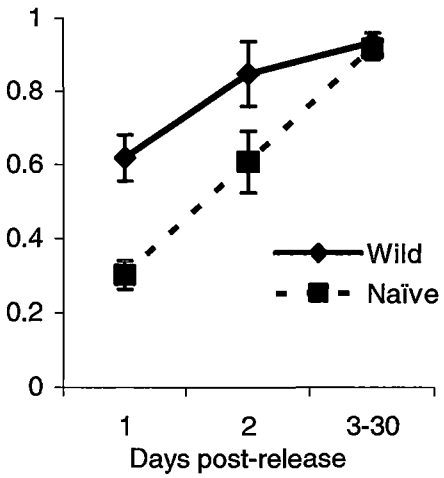


Fig. 7.5 Apparent survival estimates from Glenvar Reef recaptures with resighting from distant reef areas removed from the analysis ($\hat{c}$ =1.137).

encountering appropriate shelter is considerable and best avoided. Extensive areas of contiguous reef are clearly to be preferred as release sites.

Differences in movement rates between wild and naïve tagged lobsters clearly have the potential to influence apparent survival estimates at other sites. At all sites apart from Adventure Bay there were no detectable differences in apparent survival between groups. However, if there was greater emigration among naïve lobsters, this would lead to an underestimate of naïve lobster survival and so we cannot rule out the possibility that the survival of naïve lobsters was higher than that of wild lobsters. While we could find no well-documented instances of this in the literature, it is often suggested as a potential negative effect of hatchery releases (e.g. Hilborn & Eggers 2000, Kaeriyama & Edpalina 2004). We believe it is unlikely that naïve lobsters would out-compete wild lobsters, however targeted experiments observing interactions between wild and naïve lobsters would be required to address this uncertainty.

7.4.2 Temporal variability in survival

At three of the four sites (Adventure Bay, Safety Cove, Stapleton Point), apparent survival estimates for the 24 h to 48 h immediately following release were significantly lower than for the remaining surveys. As the effect was the same for wild and naïve juveniles, this was not the result of behavioural artefacts of the captive rearing process, but rather a response to a process affecting both groups similarly. Probable causes are either that the release method was inappropriate and lobsters were exposed to predation immediately following release and/or that both wild and naïve lobsters moved beyond the search area during the 'flight' response following release.

Immediate losses to predation in reseeding releases can be high (> 10% in 1 h for juvenile clawed lobster, Van der Meeren 2000), however experiments suggest that predation rates are low for released *J. edwardsii*. Maximum potential mortality rates of 3.5 - 5.6% for the 48 h following release were calculated from video-referenced tethering trials at our release sites (Chapter 5), and direct observations by divers and video add support to this. Lobsters were alert and responsive immediately after release, and capable of fending off all but the largest predatory fish. Video monitoring revealed that once lobsters occupied a crevice after release, they were likely to remain sheltered until night, when predation pressure is at its lowest (Oliver et al. in press, Chapter 5). Previously reported responses of predators to reseeding releases and associated diver activity include an increase in predator numbers (van der Meeren 2000, Oliver et al. in press), an increase in the activity of predators already present (Barbeau et al. 1996), or no detectable effect (Howard 1983). We observed an increase in predator activity, but few successful predation events. Male blue-throated wrasse became highly aggressive towards other large fish, particularly other wrasse, effectively reducing the number of potential predators with access to released lobsters. The agonistic behaviour of these fish reduced the time they, and other fish, could spend searching for lobsters.

Caging of lobsters for 48 h prior to release had a dramatic effect on apparent survival at Safety Cove, and a detectable (but smaller) effect at Stapleton Point. This concurs with findings for hatchery-reared abalone (Heasman et al. 2004) and sandfish (Dance et al. 2003), attributed in these cases to reduced predation pressure during the process of acclimation to release sites. In contrast, mark/recapture modelling and acoustic tracking results from Stapleton Point show that suppression of the usual 'flight' response after release, and hence lower emigration from the search area, can account for these differences.

Without further replication of caging trials we can only speculate that differences between the two sites in response to caging relate to differences in habitat structure. The reef substratum at Safety Cove consisted of stacked, small boulders providing large numbers of potential lobster shelters over the entire reef. Stapleton Point, however, provided widely dispersed areas of good quality shelter under large boulders, interspersed by rubble fields with little interstitial space. When cages were lifted at Stapleton Point, available hides appeared crowded, and many lobsters had selected the edge of the cage as the best available shelter. The small residual flight response (and corresponding reduction in apparent survival following release) observed at Stapleton Point is likely due to these lobsters redistributing to new shelter. In contrast, when cages were lifted at Safety Cove, few lobsters were seen as all were well concealed in appropriate hides within the caged area.

7.4.3 Implications of movement beyond the search area

Acoustic tracking trials provide some indication of movement patterns of lobsters beyond the range searched in mark/recapture trials, and behaviour with respect to habitat boundaries. In two acoustic tracking trials (Glenvar Reef: n=3, Chapter 3; Stapleton Point: n=6, this chapter), eight of the nine tracked naïve lobsters moved distance of between 10 and 30 m during the night following release, then occupied hides on areas of reef contiguous with the release location. The remaining lobster (chapter 3) moved in a direction where a reef/sand boundary was encountered within ca. 15 m, and once on sand the lobster continued moving until further

reef was encountered, a distance of ca. 100 m from the release site. These data suggest that lobsters that do not encounter a reef edge within a distance of ca. 30 m soon after release are unlikely to continue the 'flight' response, and will remain on the release reef.

7.5 Conclusions

Naïve lobsters of the size released in this study adapt well in the wild, avoiding predators and behaving in a similar way to wild lobsters, and with similar survival rates to wild lobsters. An exception is their propensity to ignore habitat boundaries and move greater distances when first released. While this does not effect survival on large contiguous reef areas or where there is abundant adjacent reef, it indicates that areas of isolated patch reef are not appropriate for lobster reseeding. Selecting release sites with continuous reef in a radius of at least 30 m from the release area should minimise risks associated with the observed 'flight' response on release. Other criteria used to select sites for this study, including presence of wild juveniles, abundance of appropriate shelter and high algal cover, appear appropriate.

Although seafloor cages proved a useful scientific tool for investigating lobster movement, increased apparent survival of caged lobsters was due to suppression of the 'flight' response, and therefore decreased emigration from the study site, rather than a decrease in predation rates. The added expense of releasing lobsters into seafloor cages cannot be justified for commercial releases.

Chapter 8

General discussion

8.1 Improving the efficiency of puerulus collection

Lobster aquaculture based on the collection of wild pueruli provides an opportunity to diversify aquaculture interests using high-value endemic species. Puerulus on-growing based on simple, low-technology approaches has demonstrated ability to generate economic growth in developing countries. While low labour costs may underpin profitability in developing countries, increased efficiency in puerulus collection (Chapter 2) and the development of cage-based on-growing systems (Jeffs & James 2001) enhance the potential for establishing profitable industries in other labour markets.

Hatchery production of pueruli would remove all contentious interactions with the fishing industry that is dependent on the wild lobster resource, and would ensure a stable supply of pueruli for both aquaculture and fishery restocking/enhancement purposes. However, economic hatchery production is a long-term prospect at best, because of the long larval duration. Research to-date (Kittaka 1997, A Ritar, TAFI pers comm) indicates that pristine water quality and effective pathogen control throughout larval development will be critical to improving phyllosoma survival. However, the technology and expenses associated with maintaining these pristine conditions may dictate that the on-growing of wild-caught pueruli remains the most viable option in developing and developed countries alike.

In contrast to hatchery production, puerulus collection has been shown to be economically viable (Tuan et al. 2000). An estimated 3.5 M pueruli are harvested for culture each year in Vietnam (Tuan & Mao 2004) and up to 60 000 pueruli have been collected in a year in New Zealand (Jeffs 2003). There are undoubtedly many areas globally where sufficient pueruli could be collected to establish an on-growing industry. For example, weekly averages of 20-50 pueruli and 40-80 post-pueruli per oyster crate were taken on an oyster farm comprising many thousands of crates in Luderitz, Namibia (Grobler 2001).

Possibilities for commercial puerulus collection in Tasmania remain essentially untested by industry. This situation arises because permits were issued only to aquaculture interests during a period of downturn and rationalisation in the aquaculture industry in Tasmania. Accordingly, there was little interest in funding new ventures, which by their nature involve some risk. Permit holders collected pueruli off existing structures such as salmon culture cages, but were unprepared to establish collection sites with purpose-built collectors in areas appropriate for puerulus harvest. A single attempt to do so showed considerable promise (M Ether, Jolly Roger Exports, pers comm) prior to collectors being damaged by unknown causes.

Catch rates from collectors developed in this study (Chapter 2) indicated that large numbers of pueruli could be collected in Tasmania at relatively low cost. Puerulus settlement has been monitored in a long-term project at several sites around Tasmania since 1991 (Gardner et al. 2001). Over this period, an average of 7 pueruli per month were taken from each crevice collector in the 9 months of highest settlement (June – February) at sites in eastern Tasmania (Mills & Crear 2001). Similar, if not higher yields can be expected from cheap, lightweight collectors designed for commercial use (Chapter 2). In a year of average puerulus settlement, ca. 800 collectors would be required to catch a licence quota of 50 000 pueruli. With an estimated cost of AU$20 to construct a bottlebrush collector (Chapter 2), this equates to an initial outlay for materials of AU$16 000, comparing favourably with an outlay of AU$96 000 for the same number of crevice collectors. If individual collectors last an average of 2 years, this represents expenditure of AU$0.16 per puerulus using bottlebrush collectors. The labour costs associated with removing pueruli from collectors are likely to exceed costs of collector construction, however the ability to deploy lightweight collectors on long-lines should streamline this process.

Estimated costs of puerulus harvest from this study may be overly conservative. Research in Western Australia (Phillips et al. 2001) showed that the presence of neighbouring collectors increased catch

rates, implying that collectors deployed in large numbers for commercial harvesting may catch more pueruli than identical collectors deployed in small groups for scientific trials. Servicing collectors weekly or even daily in peak settlement periods should further increase catch rates (Phillips et al. 2001).

High inter-annual variability in puerulus settlement is common to all areas where settlement has been monitored (Phillips 1986, Booth 1994, Butler et al. 2001, Gardner et al. 2001). This presents a problem for lobster farmers, as a consistent supply of product will be critical for establishing markets. The ability to deploy sufficient collectors to maintain supply in years of poor settlement will be important if the industry is to develop. Attaining this goal has been enhanced significantly by the development in this study of collectors that are inexpensive to build and efficient to deploy and service.

8.2 Managing puerulus collection through reseeding

It is critical for both established and emerging lobster aquaculture industries that management protocols simultaneously promote economic viability of aquaculture interests while protecting the wild lobster resource. Where commercial puerulus harvest is being considered in areas with an existing wild fishery for lobsters, management of puerulus harvest must be integrated with that of the wild fishery.

It is unclear whether there are any extant examples of spiny lobster aquaculture/on-growing industries that are both profitable and sustainable. We have not as yet seen profitable industries emerge in Tasmania or New Zealand, where management measures err on the side of caution in protecting the wild resource. Despite attempts at management through reseeding, the industry in the Philippines appears unsustainable due to unrestricted harvesting of all sizes of lobsters for on-growing (Arcenal 2004). The effectiveness of reseeding is predicated on seed being collected prior to mortality 'bottlenecks', and it is clearly inappropriate where larger lobsters

are collected for on-growing. The status of the industry in Vietnam is unclear. Steady declines in wild stocks (Thuy & Ngoc 2004) suggest that the total harvest of lobster (adult and pueruli) is unsustainable, although the relative contribution of each sector to this decline is unknown. Nonetheless, there is no inherent reason why, with an appropriate combination of harvest and grow-out technology coupled with effective management, this industry cannot achieve both profitability and sustainability.

Research presented here supports the use of reseeding of juveniles as an appropriate technique to compensate for the harvest of pueruli. Where release reefs were of adequate size (Chapter 7), survival of naïve lobsters was equivalent to that of released wild-caught lobsters throughout mark-recapture trials (Chapters 6, 7). Clearly behavioural responses of naïve juveniles were appropriate to endure short- and medium-term stressors (Chapter 6) on lobster survival. While mark-recapture trials provided a relative measure of survival for tagged wild and naïve lobsters, tethering trials (Chapter 5) and direct observation (Chapter 7) show absolute mortality to be very low for wild and naïve lobsters alike in the high-risk period following release. Given that behavioural changes caused by antennal tagging wild lobsters are short-lived, lasting only 24 to 48 hrs (MacDiarmid et al. 1991), the equivalence of mark-recapture survival estimates for wild and naïve lobsters beyond this period indicates high survival among naïve lobsters.

In contrast to many other hatchery-reared marine species, diver observations (Chapter 7) and video monitoring (Chapters 5, 7) revealed effective defence and escape responses among newly released juvenile lobsters confronted by predators. These responses may be innate, so that they are manifest on release to the wild regardless of conditions in on-growing systems. Alternatively, despite the absence of predators during on-growing, it is possible that avoidance responses are learnt. Lobsters become temporarily vulnerable to attack by similar-sized conspecifics in the period following moult when their exoskeleton is soft. Where adequate hides are not provided within tanks, mortality rates due to cannibalism at this stage are high (Crear et al. 2000). Thus

vulnerability after moulting may in effect provide repeated periods of 'predator conditioning', sufficient to teach lobsters how to evade attacks, and thereby equip them for release. Such conditioning would not occur in, for example, hatchery-reared finfish species, among which cooperative schooling may be more common than agonistic and cannibalistic behaviour.

Acoustic tracking (Chapter 3) coupled with visual and video monitoring (Chapters 5, 7) revealed appropriate habitat choice and use by newly released juvenile *Jasus edwardsii.* While diet composition differed between wild and naïve juveniles (Chapter 3), stomach fullness did not, and given the opportunistic nature of feeding in juvenile *J. edwardsii* (Edmunds 1995), this is unlikely to represent a threat to survival of naïve lobsters.

Given that reseeded naïve lobsters appear to survive and integrate well with wild populations, careful design of release protocols should enable effective compensation for puerulus harvest through reseeding. Survival of *J. edwardsii* juveniles will be maximised by stipulating that lobsters be released at night (Chapter 5, Oliver et al. in press) to large areas of reef where lobsters can move at least 30 m in any direction without moving off reef and onto sand (Chapter 7). Choice of release sites must be considered at multiple spatial scales. At a local scale, selection of release habitats to maximise survival of *J. edwardsii* juveniles appears fairly straightforward. Sites must have a dense macroalgal cover and provide ample hides of a size similar to the body size of released lobsters (Chapter 7). The presence of wild juveniles proved an appropriate indicator of suitable release habitat. While these criteria were not tested individually in the current study, sites selected on this basis exhibited low and uniform predation pressure (Chapter 5), and provided no disadvantage to naïve lobsters when compared with wild lobsters (Chapters 6, 7).

At a broader spatial scale, release of juveniles could be used to achieve fishery management outcomes beyond simply compensating for puerulus removal. For instance, in Tasmania releases could be used to build biomass in the NE sector of the fishery where egg

production is low, and there is little sign of recovery (Gardner et al. 2005a). Alternatively, juveniles could be returned to no-take reserve areas, as trialled in the Philippines (Arcenal 2004), further boosting egg production. However, this system would not directly achieve management aims, as reseeded juveniles remaining within the reserve would not be accessible to the fishery, and would therefore not replace those removed from the fishery as pueruli. Without a reduction in allowable catches or fishery effort, this system would place further pressure on stocks outside reserve areas. Gains in recruitment through a possible increase in egg production may offset this effect, but this is difficult to quantify for a species with such a lengthy planktonic larval stage.

Ideally, any enhancement of egg production would occur in areas that are important sources for recruitment. However, source-sink relationships for spiny lobsters in general are poorly understood because of their long planktonic phase and lack of knowledge about transport (Lipcius et al. 1997). In these circumstances the conservative approach, and the one adopted for Tasmanian puerulus harvest permits, is to require that juvenile lobsters be released back to reefs adjacent to where pueruli were collected. While this may not maximise the benefit from reseeded lobsters, it protects against the risk of releasing lobsters in sink locations, further decreasing effective spawning biomass.

Reseeding protocols must also seek to minimise the risks of genetic modification and disease introduction to wild populations. Since reseeded juveniles were originally captured from the wild, there are fewer concerns about genetic effects than are associated with releases involving hatchery-reared seed (Gaffney et al. 1996, Utter 1998). Mitochondrial DNA analysis of *J. edwardsii* from southern Australia and New Zealand showed an absence of population subdivisions throughout this region (Ovenden et al. 1992), negating any genetic risks associated with translocating lobsters. However, there may still be genetic consequences of domestication such that genotypes that would not survive in the wild are able to persist in culture. Of greater concern would be any attempt by farmers to select the slowest growing individuals from their tanks for

reseeding. This concern was addressed in Tasmanian permit conditions by stipulating a minimum size for release, based on the average size of wild lobsters at 12 months after settlement. Similarly, the risk of disease introduction from culture systems was addressed by developing a health-monitoring program involving the screening of juveniles prior to release (Handlinger et al. 1999).

In calculating the number of lobsters to be released under reseeding programs, two sources of mortality must be considered; the mortality of settling pueruli and juveniles in the year following settlement, and the mortality of reseeded juveniles over and above that of wild juveniles of the same age. Here we have shown that mortality of reseeded juveniles is low, and a conservative approach would be to release an additional 5% of lobsters captured as pueruli to account for this (Chapter 5). By comparing the number of settling pueruli in an area (estimated from catches on puerulus collectors) with subsequent postlarval abundance, Herrnkind and Butler (1994) estimated that ca. 3% of settling *Panulirus argus* pueruli survive the first year post-settlement. Independent mark-recapture trials of settling pueruli produced survival estimates for the same period of 0.6 - 4.1% (Herrnkind and Butler 1994). A mark-recapture experiment with *J. edwardsii* pueruli in Tasmania (Edmunds 1995), while limited by low numbers of recaptures, produced slightly lower although somewhat variable survival estimates.

Clearly the effective implementation of reseeding as a means of managing puerulus harvest will be greatly aided by further research providing robust estimates of post-settlement survival specific to both lobster species and location. Research currently underway may, in the near future, provide such estimates for *J. edwardsii* in southern Australia (Ibbott 2001). In the meantime, a conservative approach in setting numbers for release is prudent. For example, stipulating the release of a number of juveniles equivalent to 15% of the pueruli initially captured would replace the ca. 4% of lobsters that would have survived naturally, conservatively allow for 5% mortality associated with release, with a further 6% to allow for uncertainty in survival estimates. A total release of closer

to 10% may prove appropriate if, by further experimentation, the uncertainty associated with estimating post-larval mortality could be reduced.

Lobster culture operations may provide for some level of wild stock enhancement through reseeding, as a windfall to the wild fishery. Any pueruli released over and above the numbers required to compensate for puerulus removal will enhance the wild stock. While, in one sense, an ideal model may see the coincident enhancement of the wild fishery along with development of a lobster culture industry, stock enhancement comes at a cost to the aquaculture industry. In Tasmania a permit requirement for the release of 25% of captured lobsters following a year of on-growing has proven a disincentive to industry development. The early development of culture industries managed under this system may provide some indication of the level of enhancement that can be sustained along with profitable culture operations.

In conclusion, research presented here has identified and tested effective, low-cost methods for both puerulus collection and the sustainable management of puerulus harvest. The positive outcomes of this research, combined with further development of efficient cage-based grow-out systems, should provide the basis for sustainable development of lobster aquaculture industries in Tasmania and elsewhere.

9. References

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This CD contains video footage of tagging and field-work techniques employed during the conduct of the research reported here, as well as footage from the multi-camera system of lobster predation events (Chapters 4, 5, 7). The video footage is set up to be viewed in a PowerPoint presentation, and can be accessed via hyper-links by double clicking on the document 'Click Me.pps'